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BODY-OWNERSHIP AND VISUAL PERCEPTION

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Body-Ownership and Visual Perception

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ABSTRACT

The idea that our body plays an important role in visual perception has a long history in storytelling and philosophy. Some ideas are very intuitive. For example, few will disagree with the notion that smaller people perceive the world to be bigger, and *vice versa*, that larger people perceive the world to be smaller. In contrast, more controversial ideas regarding the role of our body in visual perception have been debated by philosophers. According to these philosophers, the very nature of visual perception lies in the fact that we have a body that moves in space. Since George Berkeley (1685 – 1753) first formalized such a fundamental role for our body in visual perception, different philosophical theories have branched out to account for the latest scientific findings.

Although experimental psychologists and neuroscientists have long neglected these intriguing philosophical accounts, the recent development of body-ownership illusions allowed for a more rigorous investigation of the supposed link between our body and visual perception. In body-ownership illusions, research participants experience an artificial body (or body-part) to be their own. These illusions allow for the dissociation between the subjective experience that your body belongs to you (i.e. body-ownership) and the mere visual impression of your body from a first-person perspective. The studies that comprise this thesis use different ownership illusions to investigate the role of body-ownership in visual perception, and the role of visual perception in body-ownership, with visual perception being an umbrella-term for both visuospatial perception and visual awareness.

In Study I and Study II we investigated the mechanisms by which body-size influences the perceived size of the world, by having participants experience ownership of different sized (and sometimes invisible) bodies. Our results show that this own-body-size effect does not rely on visual information per se, but instead, on the recalibration between visual and tactile information that updates the representation of external space. In Study III we combine the rubber hand illusion with binocular rivalry to show that body-ownership promotes visual awareness of a fake hand. And in Study IV we combine the rubber hand illusion with continuous flash suppression to show that ownership can be induced in the absence of visual awareness. Such unconscious ownership calls for a reevaluation of the standard definition of body-ownership. Taken together, these studies illuminate the intricate relationship between body-ownership and visual perception. In addition to the scientific research fields of visuospatial perception, visual awareness, and body-ownership, these results are valuable to the philosophical debate on the nature of visual perception and might provide future applications in clinical psychology.

LIST OF SCIENTIFIC PAPERS

I. **van der Hoort, B.**, & Ehrsson, H. H. (2014). Body ownership affects visual perception of object size by rescaling the visual representation of external space. *Attention, Perception, & Psychophysics, 76*(5), 1414-1428.

II. **van der Hoort, B.**, & Ehrsson, H. H. (2016). Illusions of having small or large invisible bodies influence visual perception of object size. *Scientific Reports, 6*, 34530.

III. **van der Hoort, B.**, Reingardt, M., & Ehrsson, H. H. Body ownership promotes visual awareness. *Submitted manuscript.*

IV. **van der Hoort, B.**, Radziun, D., & Ehrsson, H. H. Unconscious ownership: rubber hand illusion during continuous flash suppression. *Manuscript.*

CONTENTS

LIST OF ABBREVIATIONS

AIWS	Alice in Wonderland syndrome
AVSS	audio-visual sensory substitution
CFS	continuous flash suppression
EBA	extrastriate body area
fMRI	functional magnetic resonance imaging
HMDs	head mounted displays
IPS	intraparietal sulcus
LOC	lateral occipital complex
ORD	optical rearrangement device
PMC	premotor cortex
pRF	population receptive field
SCR	skin conductance response
TVSS	tactile-visual sensory substitution

1 INTRODUCTION

Have you ever visited the house you grew up in as a child? Or maybe been back to your old primary school? Or perhaps you found an old toy that you used to play with? If you did, you were probably surprised to see that your old bedroom appeared rather small, your old classroom was not as spacious as you remember, and your dusty teddy bear is not as big as you thought it was. These examples suggest that the world appears larger to a child. One possible explanation for this phenomenon is that we perceive the size of the world relatively to the size of our body. Poincarré (1897) illustrates this idea very clearly:

"Suppose that in one night all the dimensions of the universe became a thousand times larger. The world will remain similar to itself, if we give the word similitude the meaning it has in the third book of Euclid. Only, what was formerly a meter long will now measure a kilometer, and what was a millimeter long will become a meter. The bed in which I went to sleep and my body itself will have grown in the same proportion. When I awake in the morning what will be my feeling in face of such an astonishing transformation? Well, I shall not notice anything at all."

This thought experiment highlights how intuitive it is that our body is used as a 'fundamental ruler' in visual perception. It seems to be common knowledge, and has been utilized by some renowned literary works, such as Alice in Wonderland and Gulliver's Travels, which could each be viewed as visual perception thought experiments in their own right. Extending beyond common knowledge are the more radical claims about the relation between our body and visual perception that have been made by several philosophers, as shall be discussed in detail in section 1.2. Briefly, these philosophers argue that the very nature of visual perception is based on owning a body that moves around in space. Or to put it more boldly, that visual perception as we know it, is not possible without owning a body. Intuitive and radical ideas alike, the interaction between owning a body and visual perception has largely been neglected by experimental psychologists, mainly because it has been difficult to investigate it in a controlled laboratory setting. However, recent developments in body perception research have changed this, and allow for a rigorous examination of the importance of our body in visual perception, and thereby, provide an opportunity for testing some of these intuitive ideas and radical claims.

1.1 BODY-OWNERSHIP

When you look down at your body, you immediately recognize it as your own. And not only do you recognize it, as if you would recognize a long-lost friend or your newly bought car, it also feels like your body. The term body-ownership refers to that very sensation that your body belongs to you (Gallagher, 2000). Patients with damage to their parietal and frontal lobes sometimes lose this sensation for a specific limb (Arzy, Overney, Landis, & Blanke, 2006; Bottini, Bisiach, Sterzi, & Vallar, 2002). This clinical condition, known as asomatognosia, shows that body-ownership is the result of continuous brain activity and that

it can fail to arise if that brain activity is disturbed. Importantly, some of these patients can still feel touch, which indicates that their loss of body-ownership is not due to a lack of somatosensory processing itself. However, apart from showing that body-ownership is a brain function, these clinical observations tell us little about the general principles and perceptual mechanisms of body-ownership.

1.1.1 Rubber hand illusion

The study of body-ownership accelerated at the end of the 20th century when Botvinick and Cohen reported an illusion in which body-ownership could be transferred to an inanimate object: the rubber hand illusion (Botvinick & Cohen, 1998) (Figure 1A). In the rubber hand illusion, the right hand of a research participant lies on a table but is occluded from sight. A rubber right hand is placed parallel and medial to the participant's veridical right hand, and is fully visible. The participant observes the rubber hand while the experimenter uses two small brushes to touch the participant's veridical hand and the rubber hand at the same time (i.e. synchronous), and at corresponding locations with equal speed and direction (i.e. spatially congruent). Within a minute, the majority of participants will report a sense of ownership for the rubber hand.

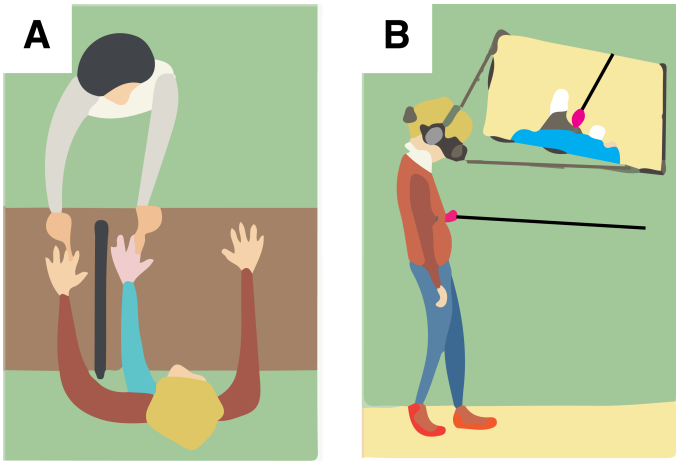

Figure 1. The rubber hand illusion (**A**) and the full-body illusion (**B**), adapted from Kilteni et al. (2015). © Konstantina Kilteni

The most straightforward way to measure ownership is to directly ask the participant. Botvinick and Cohen used a questionnaire that contains illusion statements to capture illusory ownership of the rubber hand (e.g. "The rubber hand felt like my own hand") as well as control statements to capture expectancy effects and task compliance (e.g. "It felt as if I had more than one right hand at the same time"), for which participants indicate how much they agree or disagree on a seven-point Likert scale. Most studies that investigate body-ownership use such a subjective report as a measure for body-ownership, and the original statements from Botvinick and Cohen are often re-used, or adapted to fit a particular experiment

(Kalckert & Ehrsson, 2012; Petkova & Ehrsson, 2008; van der Hoort, Guterstam, & Ehrsson, 2011). In addition to subjective reporting on a standardized questionnaire, two objective measures are often used to quantify the strength of the rubber hand illusion. After the rubber hand illusion is induced, and participants are asked to close their eyes and point towards the perceived location of their veridical hand, they point somewhere in between their real hand and the rubber hand. This phenomenon was described by Botvinick and Cohen and is known as proprioceptive drift. A second objective measure of body-ownership that is widely used is the skin conductance response (SCR) to a threat with a sharp object (e.g., Armel & Ramachandran, 2003; Petkova & Ehrsson, 2008; van der Hoort et al., 2011). After the ownership illusion is induced, the experimenter for example threatens to stab the rubber hand with a knife. Because the participant experiences ownership of that hand, this causes an autonomous fear response. Among other things, it entails increased diaphoresis, which can be measured because sweaty skin conducts electricity better than dry skin. The skin conductance response can be seen as the most objective measure of body-ownership because it occurs completely outside of awareness, and involves no active contribution from the participant. To be clear, participants are completely aware that the rubber hand is not really their hand, it is an illusion and not a delusion. Despite this knowledge, proprioceptive drift and the threat-induced SCR are surprisingly robust effects.

With their publication of the rubber hand illusion, Botvinick and Cohen (1998) provided an experimental tool for experimental psychologists and cognitive neuroscientists to study body-ownership in healthy research participants. The rubber hand illusion showed that body-ownership can be transferred to an inanimate object, and must therefore be the result of a dynamic process, which continuously deals with new information. It triggered questions such as: What are the limits of the rubber hand illusion, and what are its requirements? And what do these limits and requirements tell us about the mechanisms behind body-ownership? Most behavioral experiments on the rubber hand illusion apply manual tactile stimulation to both the participants' hand and the rubber hand, and therefore minor temporal mismatches may occur. As long as these mismatches are small enough, ownership will still be induced. However, when touches are deliberately mismatched, the rubber hand illusion is broken. In fact, asynchronously touching the two hands is a standard control condition precisely because it abolishes ownership. After a minute of asynchronous touches, participants do not subjectively report ownership, they display smaller proprioceptive drift towards the rubber hand, and they have weaker SCRs when the rubber hand is threatened (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Ehrsson, 2009; Shimada, Fukuda, & Hiraki, 2009; Tsakiris & Haggard, 2005). Thus, there seems to be a certain time window in which the two hands need to be touched: the *temporal rule*. The duration of this time-window has been investigated by increments of 100 ms, and the maximum delay that still leads to significant subjective report and proprioceptive drift was found to be 300 ms (Shimada et al., 2009). The second rule of the rubber hand illusion is its *spatial rule*. Touching the index finger of the participant while touching the middle finger of the rubber hand does not induce ownership. The touches need to be spatially congruent (Costantini & Haggard, 2007; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013). This also means that the direction and speed of the

touches need to match. A third rule is the *perspective rule*. The rubber hand needs to be placed parallel to the participant's real hand. Rotating the rubber hand disrupts the illusion. And again, as for asynchronous stimulation, rotating the hand is often used to deliberately disrupt ownership of the rubber hand (Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004). However, because the rubber hand cannot physically be in the same location as the participant's real hand, a certain amount of lateral displacement is allowed for. The lateral displacement at which the rubber hand illusion seems to break down is approximately 27.5 cm (Lloyd, 2007). A fourth and final rule is the *anatomical rule*. The rubber hand must be shaped as a hand and not as a non-corporal object such as a giant broccoli. Control experiments have used objects less adventurous than broccoli to replace the rubber hand, such as a block of wood or a stick, but ownership cannot be induced for an object that does not resemble a hand (Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005).

These four rules (temporal, spatial, perspective, and anatomical) need to be met in order to induce the rubber hand illusion. What does this tell us about the perceptual mechanism of body-ownership? Each of these rules provide evidence for the idea that (illusory) body-ownership depends on multisensory integration (Stein & Stanford, 2008). Multisensory integration refers to the process of binding two or more senses together into a single percept. For example, when you see a dog barking and you hear a barking sound, providing the two are synchronous (temporal rule) and from the same location (spatial rule), you will perceive a barking dog, i.e. visual information is integrated with auditory information to form one multisensory percept. Ownership depends on multisensory integration of vision, touch, and proprioception, creating the multisensory percept of a hand that belongs to you (Ehrsson, 2012; Kilteni, Maselli, Kording, & Slater, 2015). In the rubber hand illusion, touch applied to the real hand is integrated with the visual appearance of the rubber hand being touched, which leads to the perception that they both relate to the same event, i.e. that they are the same touch. This phenomenon is known as referral of touch, and is one of the hallmarks of ownership illusions that rely on visuotactile integration. It follows the temporal rule and the spatial rule described above. The perspective rule is the rule for integrating vision and proprioception. Visual information of the orientation and location of the rubber hand needs to be integrated with the perceived location of the own hand. As described above, such integration can overcome spatial discrepancies of approximately 27.5 cm. The anatomical rule can also be interpreted as the congruence between visual and proprioceptive information. The proprioceptive sensation of having five fingers for example, only allows for the embodiment of an inanimate object with five fingers (e.g. a rubber hand).

Visuotactile stimulation is not the only way in which ownership for the rubber hand can be induced. Another possibility is to synchronize movement of the rubber hand with movement of the real hand (Kalckert & Ehrsson, 2012, 2014). In the moving rubber hand illusion, the index finger of the rubber hand, in view, is connected to the index finger of the participant's hand, which is occluded. When the participant moves their finger while looking at the rubber hand that moves synchronously, ownership of the rubber hand is induced,

including proprioceptive drift and a SCR to a knife threat. This moving rubber hand illusion follows the same four rules as the original rubber hand illusion. In the case of active (intended) movement, the illusion results from the integration of intention (or efference copies) with vision and proprioception.

1.1.2 Full-body illusion

Since the rubber hand illusion, transferal of ownership to an alien object has been extended to ownership of an entire artificial body (Petkova, Björnsdotter, et al., 2011; Petkova & Ehrsson, 2008) (Figure 1B). In the full-body illusion, the participant wears a set of head mounted displays (HMDs) that are connected to two cameras facing down a mannequin (Figure 1B). The result is a first-person perspective of the mannequin's body in 3D. The experimenter now touches the participant's body and the mannequins body synchronously and spatially congruent. As in the rubber hand illusion, integrating the seen touch and the felt touch leads to the sensation that they are part of the same touch (referral of touch), and leads to ownership of the mannequin's body, including a SCR to a knife threat (Petkova & Ehrsson, 2008; van der Hoort et al., 2011). One difference with the rubber hand illusion is that there is no incongruence between proprioception and vision. The mannequin's body is located where you sense your own body to be, so in contrast to the rubber hand illusion this discrepancy does not need to be resolved. As a consequence, proprioceptive drift cannot be measured in the full-body illusion. The full-body illusion relies on the same multisensory mechanism as the rubber hand illusion (Ehrsson, 2012; Kilteni et al., 2015). It therefore follows the same four rules of ownership, but with the anatomical rule referring to the necessity of a body shape instead of a hand shape (Petkova & Ehrsson, 2008; Petkova, Khoshnevis, & Ehrsson, 2011).

1.1.3 Role of vision in body-ownership

The rubber hand illusion exemplifies the dominance of visual information in body-ownership. Proprioception is recalibrated towards the visual location of the rubber hand (i.e. proprioceptive drift), and tactile sensations are attributed to visual events on the rubber hand (i.e. referral of touch). Interestingly, the mere sight of a rubber hand from a first-person perspective in the absence of tactile stimulation can elicit proprioceptive drift, but not the subjective sensation of ownership (Rohde, Di Luca, Ernst, Gibson, & Bradshaw, 2011). Furthermore, when the visuoproprioceptive mismatch between the rubber hand and the real hand is abolished by using a 'mirror-box' such that the rubber hand appears at the exact proprioceptively perceived location of the real hand, the subjective sensation of ownership is instant (Dunphy, Evans, Klostermann, & Durgin, 2005). Another study found that in the absence of touch, a laser light moving over the rubber hand, could elicit the sensation of touch or heat (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007), which suggests that the visual appearance of touch can trigger tactile sensations. Taken together, these observations show that visual awareness is often the most important sensory modality in body-ownership.

In addition, there seem to be a few purely visual restrictions on body-ownership, such as the perspective rule and the anatomical rule. To embody an object, the object's shape and orientation matter. We cannot embody a giant broccoli, especially if it's lying rotated on our plate. But as long as the perspective rule and anatomical rule are met, ownership illusions are rather flexible regarding visual input. For example, skin color does not affect the strength of the rubber hand illusion (Farmer, Tajadura-Jiménez, & Tsakiris, 2012), and participants can feel ownership of a body of the opposite sex (Petkova & Ehrsson, 2008). Furthermore, the size of a rubber hand does not have to match the size of the participant's hand, although it appears easier to induce the illusion for larger hands than for smaller hands (Marino, Stucchi, Nava, Haggard, & Maravita, 2010). And, as will be discussed in more detail in section 1.2, ownership can be induced for bodies as small as 30 cm and as large as 400 cm (van der Hoort et al., 2011).

However, one recent development in body-ownership research challenges the anatomical rule. In the invisible hand illusion there is no rubber hand in front of the participants (Guterstam, Gentile, & Ehrsson, 2013). Instead, the experimenter is stroking in empty space while simultaneously stroking the participant's occluded hand. The strokes in empty space outline the shape of a hand, and spatial congruency is maintained when stroking different fingers of the 'invisible hand'. The tactile sensations are integrated with the visible moving brush, such that the touches seem to arise from empty space, and thus, that the participant now owns an invisible hand. The invisible hand paradigm is applicable to full-body illusions as well, inducing an invisible body illusion (Guterstam, Abdulkarim, & Ehrsson, 2015). These illusions follow the same rules of ownership as discussed above, except for the anatomical rule. Because of its shape, it seems unlikely that an invisible giant broccoli illusion could be induced, but this shape restriction could be explained by the spatial rule.

Despite the dominance of vision in body-ownership, it seems unlikely that visual perception of our body is necessary for body-ownership, since this would imply that blind people cannot have body-ownership. In the absence of visual information, body-ownership can result from the multisensory integration of the remaining senses, such as proprioception and touch. In a variation of the rubber hand illusion in which participants are blindfolded (Ehrsson, Holmes, & Passingham, 2005), the veridical right hand is touched by the experimenter, while the left hand of the participant is guided to synchronously touch a rubber hand. This causes the sensation that participants are touching their own hand. Interestingly, this procedure is not effective in blind people (Nava, Steiger, Röder, Spence, & Röder, 2014; Petkova, Zetterberg, Ehrsson, Farne, & Roland, 2012), probably because they rely more on proprioception and touch in everyday life, making it harder to fool those senses.

Returning to the role of vision in body-ownership, ownership illusions that rely on visuotactile and visuoproprioceptive congruencies have done so in the realm of conscious vision. However, awareness might not be necessary for multisensory integration, as has been shown for visual and auditory stimuli (Faivre, Mudrik, Schwartz, & Koch, 2014). Thus, if multisensory integration of vision, touch, and proprioception is sufficient for ownership,

awareness of those senses might not be needed. In Study IV, which will be introduced in more detail in section 1.3, we investigate the necessity for visual awareness in the visuotactile rubber hand illusion. In contrast to investigating the mechanisms of body-ownership themselves, the other studies that comprise this thesis examine the role of body-ownership on visual perception. Thus, the body-ownership illusions described in this section are used merely as a method to study an entire different field of research. The role of the body and body-ownership in visual perception will be discussed in the following sections.

1.2 VISUOSPATIAL PERCEPTION

1.2.1 Visual-cue approach

Visuospatial perception concerns the visual perception of size and distance. It is important for our brain to know the size and distance of objects, for knowing how to move in order to interact with those objects, but also for identifying them – imagine mistaking a model car for a real one, or worse, the other way around. This does not seem a very complicated task. We look at something, and we immediately sense how big it is and how far away it is.

Indeed, from a computational point of view, and given that our eyes and brain are close to perfect – which they are not – this is a simple calculation (Mckee & Smallman, 1998). When we look at an apple, both eyes have a retinal image of that apple that they send to the brain. The apple's retinal size refers to the surface of the retina that receives light reflected from the apple. As you bring the apple to your mouth, its retinal size increases. This does not mean that it now appears larger, because your brain is quite familiar with the concept of size constancy, i.e., that objects don't really grow as they move towards you, but that their retinal size increases with proximity. So, if the brain would know the distance of an object with a certain retinal size it would also know its actual size. According to this simple computational model, the only necessary information to calculate the distance of an apple is to assess its so-called binocular disparity. Our two eyes are not in the same location and therefore have a slightly different retinal image of the apple. Alternate observation of an apple with only your left eye and with only your right eye, shifts the apple from the right to the left side of your visual field. If the apple has very different locations in the two retinal images, it must be nearby. Thus, the brain can use binocular disparity to calculate the apple's distance, and by combining that with the retinal size, it knows its actual size. Problem solved. However, our visual system is not a video camera attached to a computing device. And combing retinal size with binocular disparity to calculate size and distance only works for objects within one meter from the observer (Leibowitz & Moore, 1966). So, unless you're actually eating the apple, it would be hard to see its size and distance, if you were a camera attached to a simple computing device.

But the human visual system is not a simple computer, it is at the very least a complex computer. It can use all kinds of different visual information, other than retinal size and binocular disparity. In fact, traditional textbooks on visuospatial perception use the visual cue

approach to emphasize that different visual cues work together to give a sense of distance, which can be combined with retinal size to calculate physical size (Cutting & Vishton, 1995; Goldstein & Bruce, 1999). Three categories of visual cues can be dissociated: pictorial cues, motion-based cues, and oculomotor cues. Pictorial cues are visual cues of depth that can be extracted from the content of the visual image you observe. These cues are all monocular cues, i.e. the information from one eye is sufficient to extract them. Pictorial cues are well known, mainly because they are important for (realistic) art and photography since they give the impression of depth to an otherwise two-dimensional object. At least seven pictorial cues can be dissociated. Linear perspective is used to describe the fact that parallel lines convergence to a single point on the horizon (O'Leary & Wallach, 1980). When driving a car, the visual system can use this knowledge to estimate the size of a car in the distance by calculating the ratio by which the sides of the road have converged near its location. Texture gradient is the fact that the detailed texture of certain surfaces seems to get denser with distance (Bajcsy & Lieberman, 1976). Let's stay in the car but take a left turn onto that gravel road. Texture gradient refers to the individual pebbles that seem to get smaller and more densely packed the further you look. A third pictorial cue is clarity (Mather & Smith, 2002). Objects in the distance appear unclear because of small distortions caused by dust particles, fog, or warm air. This phenomenon is sometimes referred to as aerial perspective. A fourth cue is occlusion, which simply refers to the fact that farther objects can be (partially) occluded by nearer objects. The fifth cue is the height on a plane of an object (Dunn, Gray, & Thompson, 1965), which informs us about its distance because an object further away is displayed "higher" on the retina, or closer to the horizon. A sixth cue is relative size: if two objects are of identical size, the relative size of one versus the other informs the visual system about their relative distance from the observer (Hochberg & McAlister, 1955). When both of your kids accidentally let go of their helium-filled balloon, you might be able to comfort them by stating how much further one balloon is than the other, based on their relative retinal size. To increase their joy even further, you could lecture them on how the speed of an individual balloon can be assessed by using the relative size cue for the same balloon from one moment in time to the next, because that balloon is not coming back (see below). The last pictorial cue is familiar size, which is the most relevant cue for this thesis. The familiar cue works by having knowledge of the size of an object that is located in close proximity to an object of unknown size (Hochberg & Hochberg, 1952). Imagine observing a tree from a distance; its actual size is much easier to perceive if someone is standing next to it, because you know what the height of the average human being is.

We do not perceive the world as a series of still images from which we extract pictorial cues. Therefore, in addition to pictorial cues, there are additional cues that do not specifically depend on the content of an image, but instead on motion of the object or the observer. Motion parallax is a distance cue derived from movement of the observer (Rogers & Graham, 1979). When an observer moves, such as when driving a car, stationary objects in the distance move more slowly over the retina than objects nearby. Another visual cue that is based on motion uses the change of an object's retinal size. When an object is moving towards the observer, such as when a ball is approaching through the air, its retinal size increases. This

change in retinal size informs the visual system about the speed of the approaching object, and thereby also about its distance. This also works for departing objects, such as your kids' ascending balloons. This cue is called depth from motion, or more descriptively 'depth from optical expansion' (Swanston & Gogel, 1986). A third motion-based cue is the kinetic depth effect (Wallach & O'Connell, 1953). The three-dimensional shape of an object is perceived from how its two-dimensional shape changes as a result of movement of that object (e.g. a rotating wire cube). However, this cue is not strictly speaking a distance cue, i.e. it allows objects to be perceived as three-dimensional but does not inform the visual system about their distance.

A third category of visual cues is derived from the muscles that control the eye and its lens: oculomotor cues. Despite the fact that these cues are not visual in nature, they are still considered visual cues since they are part of the visual system. The ciliary muscles that cause flattening of the lens (i.e. accommodation) send signals to the visual system and are informative of the distance of an object in focus (Fisher & Ciuffreda, 1988). Similarly, the eye-converging muscles can be informative of distance because a nearby object requires more eye-convergence than a distant object (Brenner & van Damme, 1998).

The key to the visual cue approach is that all of these cues work in unison, and their relative contribution is different at different distances (Cutting & Vishton, 1995). Some cues are only informative at very short distances (e.g. accommodation), whereas others are only informative at greater distances (e.g. clarity). Occlusion is arguably the most potent distance cue, because it is effective at all distances. Although the visual-cue approach is still propagated in most vision textbooks when explaining spatial perception, alternative theories exist. The main objection of these alternative theories is that the visual-cue approach implies too strict a distinction between sensory input and motor output. To put it differently, we are not a video camera attached to a complex computer. We are our body. Our body acts and our body perceives. It perceives to act, and it acts to perceive. The following sections will discuss different approaches as to how our body and its actions are fundamentally part of visual perception in general and visuospatial perception in particular.

1.2.2 New theory of vision

The role of the body in visual perception has been debated for at least 300 years, and most scholars acknowledge George Berkeley to have started this debate when he wrote *An Essay Towards a New Theory of Vision* (Berkeley, 1709). In this essay, he provides three arguments for how the body plays an important role in visual perception. First, Berkeley claims that to perceive a distance as such, is not a purely visual phenomenon. Instead, the perception of depth comes from the association of a certain distance with a certain pattern of movement, which in turn is associated with tactile and proprioceptive sensations. His second point states that vision is not only necessary for guiding preselected actions, but vision in itself motivates certain behaviors. A looming ball motivates trying to catch it, or step away. And thirdly, oculomotor information regarding eye-convergence and lens-accommodation are important distance cues, which, as mentioned above, have been adopted by the visual-cue

approach. In the centuries that followed, the idea that the body plays a fundamental role in visual perception was never really abandoned. However, exact formulations and conceptualizations would change with new empirical findings. Since the 20th century, at least two different approaches to the embodiment of visual perception can be identified: sensorimotor contingency theories and efferent readiness theories.

1.2.3 Sensorimotor contingency theories

According to sensorimotor contingency theories, the nature of visual perception is to know how sensory input will change with movement. To really understand this stance, it is important to understand the problem of visual direction constancy. When we visually perceive our environment, even if we think we are not moving, our eyes are still performing saccades: fast and automatic eye-movements between short periods of fixation. The entire visual field sweeps over our retina, from left to right and back again, with the speed of a saccade (900 degrees per second). However, our visual perception remains stable, we do not perceive the entire world to move around chaotically. According to the *efference copy theory* (von Helmholtz, 1925; von Holtz & Mittelstaed, 1950), the solution to this problem is efference copying. The idea being that when a motor command is sent to the eye-muscles to perform a saccade, an efference-copy is send to the visual system containing information about the direction and magnitude of that eye-movement, which is then used to cancel out any changes in retinal activation that are the result of the saccade. As elegant as this efference copy solution seems, it cannot entirely explain why saccades do not lead to apparent motion (Bridgeman, Hendry, & Stark, 1975; Bridgeman & Stark, 1991). For example, in a completely dark environment a static light spot appears to move (the autokinetic effect; Levy & John, 1972). As an alternative to this strict efference copy theory, efference copies have been suggested to guide attention towards the post-saccadic position of a 'landmark object' (Bridgeman, 2010; Deubel, Schneider, & Bridgeman, 2002) so as to assess if that landmark object has moved during a saccade or not. If after the saccade, the landmark object is in close proximity to its predicted location, it was probably stationary in external space. A final possible role of efference copies is to shift receptive fields, i.e. they can cause a spatial remapping of individual neurons (Duhamel, Colby, & Goldberg, 1992).

The *reafference theory* differs from the previously discussed efference copy theory in that efference copies are not simply cancelling out eye movements, but instead serve as a cue to tap into the stored knowledge of the sensory consequences of movement (Held, 1961). Movement in this sense is not restricted to saccades but applies as well to slow eye movements, head movements, and body movements. What is crucial about this theory, is that this knowledge is acquired in the past. We have all learned that if our head rotates to the right, our entire visual field moves to the left, except if we are fixating on a moving object, such as a car. The reafference theory further states that an important function of knowing how movement will affect future sensations is that of visually guided movements. The experimental method that contributed most to this idea of learned sensory consequences of (intended) movement is that of optical rearrangement devices (ORDs): a set of goggles that

can either rotate, reverse, or laterally displace the entire visual field. George Stratton was the first to experiment with such devices, on himself (Stratton, 1897). He wore a set of inverting ORDs for eight consecutive days: his world was upside down. Initially he was not able to perform any motor task whatsoever, but gradually his vision improved, and at the end of the experiment his visual world appeared "right side up" and "in normal position". A few decades later Helmholtz performed experiments with ORDs that cause lateral displacement (16-18 degrees to the left) of the visual field to study reaching behavior (von Helmholtz, 1925). After the initial overshoot in reaching, adaptation took place and reaching was as accurate as before wearing the goggles. Interestingly, this adaptation also transferred to the other hand, which he had not trained in the reaching task, which suggests a general visuomotor recalibration. After removing the ORD, an aftereffect in the opposite direction occurred. A few decades later it was found that such adaptation occurs when there is active movement but not when there is solely passive movement (Held & Hein, 1958). Others however have found adaptation after passive movements (Singer & Day, 1966) and even in the absence of movement (Howard, Craske, & Templeton, 1965; Kravitz & Wallach, 1966). Critics of the reafference theory have proposed that ORD-induced adaptation occurs as a result of visuoproprioceptive conflict itself rather than reafferent visual information. According to these critics, increased adaptation after (active) movement is the result of a (greater) conflict between where the hands are visually perceived to be and where they are proprioceptively felt to be (Harris, 1965; Welch, 1978). Furthermore, what seems to be adapting is not visual perception, but proprioception. When Stratton (1897) claimed that the world appeared "right side up" and "in normal position" he did not mean that the floor was down and the ceiling up again. Instead, he meant that he would feel an object (by touch) where he visually perceived it to be, that things made sense again. The proprioceptive information from movements stayed the same, but the meaning assigned to that information changed by the recipient brain areas. They now signify a movement in the distorted visual space, instead of the normal visual space (Harris, 1965).

The *enactive approach* is the most contemporary theory on sensorimotor contingency, and can be viewed as an extension of the reafference theory. One major difference is that the enactive approach does not assume that the function of visual perception is to guide motor behavior (Noë, 2004). Instead, conscious visual perception itself depends on learned contingencies between movement and subsequent changes in visual information. According to Noë, the perception of a three-dimensional object, i.e. the perception of it being voluminous, starts with the visual appearance of that object as a two-dimensional patch: of it having a certain "perspective-shape" (P-shape) and a certain "perspective size" (P-size). Only in combination with the understanding of how P-shape and P-size would change with movement can the object be perceived for what it really is: its three-dimensional shape and size. For example, if you look at a table from a certain angle, it appears as a trapezoid with two legs, which is its P-shape. Knowing how this object would change its P-shape with movement is necessary for perceiving its actual three-dimensional shape. It is important to note that this does not mean that active behavior needs to take place, or even that the object allows for certain behavior. In addition to ORDs, the enactive approach uses observations

from another important experimental method, which was not available at the time of the reafference theory, known as tactile-visual sensory substitution (TVSS) (Figure 2). As its name implies, TVSS is the replacement of visual perception with that of tactile perception, often in people who are blind, in such a way that visual space can be perceived by touch (Bach-y-Rita, 2004; Bach-y-Rita & Kercel, 2003; Maidenbaum, Abboud & Amedi, 2014; Sampaio, Maris, & Bach-y-Rita, 2001). A TVSS-device consists of a matrix of electrodes attached to a person's body, which gives tactile stimulation in response to input from a low-resolution video camera. At first, sensations from such a device are purely tactile in nature. However, after extensive training most people do not perceive the tactile sensations anymore, but instead report to have vision-like experiences of objects in external space. These people can report the size, shape and location of an object, and even perform simple visuomotor tasks. They can "see" with touch. Similar findings have been found for audio-visual sensory substitution (AVSS) (Bach-y-Rita, 2004; Bach-y-Rita & Kercel, 2003; Maidenbaum et al., 2014; Ward & Meijer, 2010). AVSS-devices convert brightness to loudness, and the spatial location to frequency. After a few months of training, this leads to similar vision-like experiences of objects in external space, such that blind people can see with their ears. The crucial observation for the enactive approach, is that active training is required to obtain these results of TVSS and AVSS. Self-initiated movement is necessary for learning the change from sensorimotor contingencies specific for touch or sound to the sensorimotor contingencies specific for vision (Hurley & Noë, 2003).

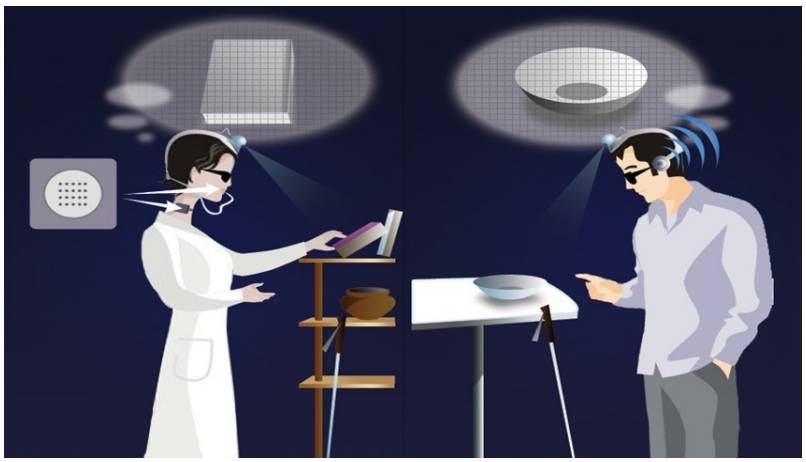

Figure 2. Tactile-visual sensory substitution (left) and audio-visual sensory substitution (right), adapted from Maidenbaum et al. (2014). © Amir Amedi

1.2.4 Efferent readiness theories

Efferent readiness theories of visual perception state that an integral part of seeing is that it triggers preparation of action, instead of the preparation of action merely being a consequence of vision (Taylor, 1962, 1965, 1968). Patients with frontal lobe damage sometimes display automatic behavior that is associated with a certain object (Frith, Blakemore, & Wolpert, 2000). Seeing a bottle of water and a glass will make these people pour the glass with water whether they are thirsty or not. Healthy individuals do not display

such automatic behavior but that does not mean that there is no 'efferent readiness' to do so. Neuro-scientific studies show that perception of an object is accompanied by a preparedness of the motor system to act upon that object (Jeannerod, 2006; Rizzolatti & Sinigaglia, 2008).

According to one recent version of such theories, the *disposition theory*, sensory information only leads to spatial perception if it triggers some behavioral disposition. To determine the spatial location of an object, sensory input and possible motor programs are both required (Grush, 2000, 2007). The main idea is that sensory information and motor planning are both formulated in terms of egocentric spatial coordinates. This means that space perception is where sensory input and motor output meet, and therefore space itself is represented holistically as a combination of the two. And thereby, the representation of space provides a framework (or language) for the brain's input and output to communicate in.

Another good example of an efferent readiness theory is the *ecological perception theory* (Gibson, 1977, 1979). Its unique character is based on the emphasis of bottom-up processes, in contrast to top-down theories of vision (e.g. representationalism). According to this theory, the optical environment is informative in and of itself, without the need for a Cartesian observer to interpret that information. Therefore, ecological perception is also known as 'direct perception'. Gibson uses the term invariants for those aspects of our optical environment that contain valuable information without the need for a top-down interpretation of them. In this sense, most visual cues described in 1.2.1 can be viewed as invariants. However, a more radical claim, which is relevant here, is that visual perception is essentially the interaction between an animal and its environment (hence 'ecological perception'). Gibson (1977) introduces the term affordances to describe the nature of visual perception. Perceiving an object is perceiving what that object affords us to do (e.g. Mark, 1987; Warren, 1984; Warren & Whang, 1987). A flat surface affords one to sit on it, a handle on a cup affords one to grasp it, etc. Crucially, different animals have different affordances and therefore perceive the world differently. And similarly, different people perceive the world differently because their environment contains different affordances. If an adult sees a four-feet vertical elevation it affords for climbing, whereas a small child does not perceive this affordance but instead might perceive it as to afford for leaning. Thus, the physical properties of the observer define how objects in external space are perceived. For example, spreading your arms makes an aperture appear narrower because it does not afford to walk through it with that posture (Stefanucci & Geuss, 2009). Similarly, increasing one's action radius by holding an elongated tool makes distances appear shorter (Witt, Proffitt, & Epstein, 2005).

An elaboration of the role of affordances, or 'action possibilities', on visual perception has been proposed by Proffitt (2006). According to Proffitt, perception is not only influenced by what types of actions the environment allows for, but also the energy costs of those actions, as well as our individual skills to perform those actions. For example, wearing a heavy backpack makes hills appear steeper (Bhalla & Proffitt, 1999) and distances appear greater (Proffitt, Stefanucci, Banton, & Epstein, 2003), because it costs more energy to climb that hill or to walk that distance when wearing a backpack. Similarly, fatigued individuals and unfit people

perceive the slope of a hill to be steeper (Proffitt, Bhalla, Gossweiler, & Midgett, 1995). In addition, skills can affect visual perception. Skilled baseball players perceive the baseball to be larger (Witt & Proffitt, 2005) and skilled golf players perceive the hole to be larger (Witt, Linkenauger, Bakdash, & Proffitt, 2008).

1.2.5 Own-body-size effect

Each of the different embodied perception theories described above would predict that a child perceives the world as being larger, i.e. that the perceived size of the world is inversely related to the body size of the observer. However, these theories differ with respect to the underlying mechanisms of such an effect. Sensory motor contingency theories would claim that the (potential) movement of a child has different sensory consequences than that of an adult. Efferent readiness theories and the ecological approach however, would state that the body of a child allows for, or affords, different potential action. And according to the action-costs based perception, a child would perceive the world to be larger because a child requires more steps to cover a certain distance. However, apart from anecdotal evidence, until recently it had not been possible to directly test the intuitive prediction that the perceived size of the world is inversely related to the body size of the observer. How can we manipulate body-size in a controlled experiment? The answer has been given in section 1.1: body-ownership illusions.

Six years ago we published a variation of the full-body illusion in which we replaced the adult-sized artificial body (180 cm) with a small doll (80 cm: small-body illusion; Figure 3A) or a giant custom-made artificial body (400 cm: large-body illusion; Figure 3B) (van der Hoort et al., 2011). Using ownership questionnaires and SCRs to a knife threat, we established that ownership for these bodies is possible. Similar to the traditional full-body illusion, ownership was abolished by asynchronous visuotactile stimulation. Logically, in these versions of the full-body illusion it is crucial that brushing of the artificial body is scaled to its size, such that the small doll receives shorter strokes, and the giant body receives longer strokes, than the strokes given to the participant's veridical body. In subsequent experiments, we tested participant's perception of object size and object distance during these illusions. To this end, participants

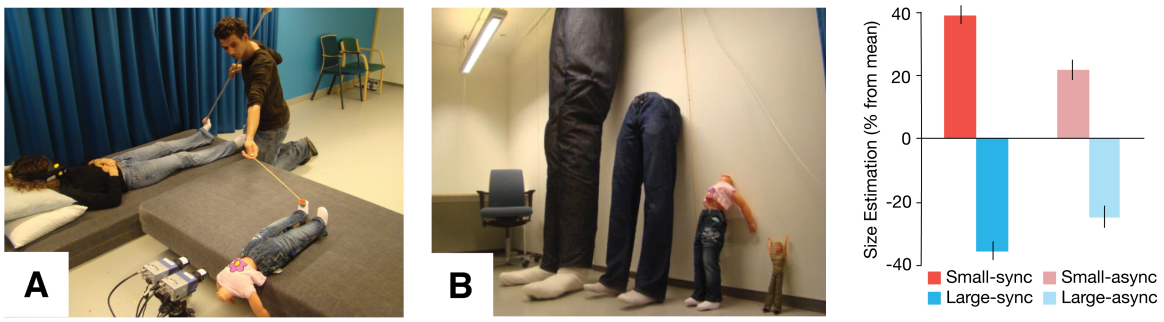

Figure 3. Small-body illusion (**A**), different sized bodies (**B**), and bimanual size estimations for small body vs large body, and synchronous vs asynchronous visuotactile stimulation. Adapted from van der Hoort et al. (2011).

were lying on a bed because it enabled them to see their body while being able to see a large part of the testing room. Because we wanted to rule out any contribution of visual cues (e.g. linear perspective, height on a plane, etc.), the height of the cameras that looked down on the artificial body was identical in the small-body illusion and the large-body illusion. As a consequence, the small artificial body needed to be elevated by placing it on a bed, while the large artificial body was lying on the ground, such that they had an identical first-person perspective (i.e. the angle from which they observed the artificial body).

In two different experiments, participants verbally estimated the size of target objects, or they used their hands to indicate the perceived size of target objects (i.e. bimanual size estimation). In two other experiments, they verbally estimated the perceived distance of target objects or they walked the perceived distance while blindfolded. Verbal report can be considered a more explicit measure of size and distance perception, whereas bimanual estimations and walking distance are more implicit measures, however both measures gave similar results. As expected, participants perceived the size of target objects to be larger during the small-body illusion and smaller during the large-body illusion (Figure 3, right panel). And similarly, they perceived the distance of target objects to be greater during the small-body illusion and shorter during the large-body illusion. Crucially, these effects were significantly diminished when ownership was disrupted due to asynchronous visuotactile stimulation. Thus, ownership was necessary to maximize the effect of body-size on the perception of object size and distance. Therefore, we proposed the term *own-body-size effect* to describe this pattern of results. In Study I and II we investigated the possible mechanisms by which ownership might affect visuospatial perception.

Other studies have described similar body-scaled effects on visual perception. The visual distortion of a participant's veridical hand affects the perceived weight of objects by following the size-weight illusion, i.e. smaller objects are perceived to be heavier despite equal weight (Haggard & Jundi, 2009). Furthermore, changing perceived hand size in a virtual reality environment inversely changes the apparent size of objects close to the hand (Linkenauger et al., 2013). And embodying a child-like avatar in a virtual reality environment causes objects to be perceived as larger (Banakou, Groten, & Slater, 2013). These findings are in line with the own-body-size effect, and therefore strengthen the conclusion that the perceived size of the world is inversely scaled to the body size of the observer.

1.3 VISUAL AWARENESS

Having discussed the spatial content of visual perception, and how our body plays a key role therein, we now turn to another fundamental aspect of vision, visual awareness. Visual awareness is a major topic in philosophy, psychology and neuroscience. It is not only studied for understanding visual awareness per se, but also for understanding consciousness in general (Crick & Koch, 1998; Lamme, 2006). The reductionist neuroscientist believes that the basic neural processes that underlie visual awareness, apply to other sensory modalities as well, and

even apply to the awareness of higher cognitive functions, such as self-awareness (Crick & Koch, 1998). How these different 'awarenesses' are bound together to create one unitary consciousness is only a follow-up question, i.e. the binding problem is a secondary problem. Similarly, to understand visual awareness of the simplest visual stimulus, such as a horizontal line, is to understand visual awareness of the rich scenes we perceive during everyday life, i.e. their difference lies in the complexity of the stimulus, not in the complexity of their underlying mechanisms. Creating a unitary conscious percept of a visual scene from simple elements of visual awareness is merely another version of the binding problem. Therefore, given the popularity of the reductionism among neuroscientists, the study of visual awareness is often a synonym for the study of consciousness. To be clear, despite the importance of visual awareness research in the search for the neural correlates of consciousness (Crick & Koch, 1998), this thesis will focus on visual awareness itself. The remainder of this section will focus on two phenomena that are often used to study it: binocular rivalry and continuous flash suppression.

1.3.1 Binocular rivalry

In binocular rivalry, each eye is presented with a different (incompatible) image. Instead of those images being fused into a single percept, such as in normal stereoscopic vision, conscious visual perception alternates between the two images roughly every few seconds. For example, presenting the image of a face to one eye, and the image of a house to the other eye, might initially result in the conscious perception of the face. At this moment, the face image is said to be dominant, and the house image to be suppressed. After a few seconds, perception switches to the house, and the face is suppressed. These perceptual switches continue to occur infinitely at irregular intervals (following a gamma distribution; Levelt, 1965). Thus, during binocular rivalry conscious perception alternates despite constant visual input (Figure 4).

Crucially, these alternations occur automatically and cannot be stopped by will. Instructing participants to keep one image dominant as much as possible renders only small and unreliable shifts in the overall dominance of that image (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). Because of this automaticity, binocular rivalry has been hypothesized to occur relatively early in visual processing. In line with this hypothesis, fMRI studies have found that activity in the primary visual cortex reflects conscious perception

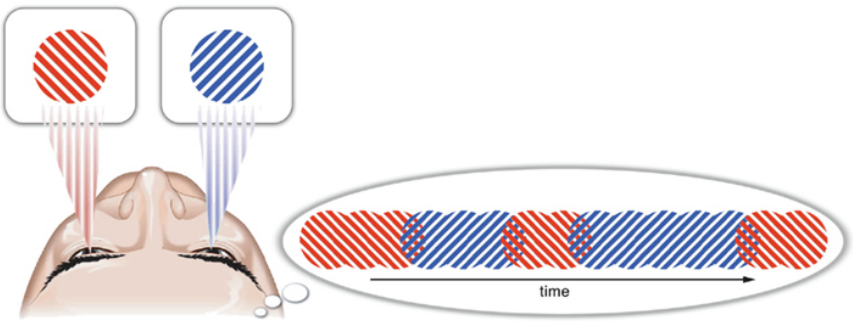

Figure 4. Binocular rivalry. Adapted from Dieter & Tadin (2011).

during binocular rivalry (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). Furthermore, when the images presented to each eye are reversed during ongoing rivalry, the dominant eye remains dominant (Blake, Westendorf, & Overton, 1980; Lee & Blake, 2004), such that perception switches to the image that is now presented to the currently dominant eye. This suggests that the two eyes are competing for awareness, and that competition must be resolved "early" by neurons that receive monocular input. However, there is also evidence for competition at a later stage of visual processing. Activity of neurons at later stages of visual processing, which invariably receive binocular input, correlate much more with the ongoing percept than neurons at early stages (Logothetis & Schall, 1989; Logothetis, Leopold, & Sheinberg, 1996). In addition, reversing the visual input to each eye back and forth very quickly (5 Hz) results in normal rivalry durations (Logothetis et al., 1996). This suggests that not the eyes, but instead the images themselves are competing. Indeed, presenting each eye with complementary patchworks of two images results in the rivalry of those images, and not of the two patchworks (Kovács, Papathomas, Yang, & Fehér, 1996). These seemingly contradicting findings are accounted for by contemporary models of binocular rivalry that argue for multiple sites of competition at different stages of visual processing (Tong, Meng, & Blake, 2006).

What makes a visual stimulus more dominant during binocular rivalry? Levelt (1965) introduced the term *stimulus strength* to refer to those aspects of the visual stimulus that make it more dominant. In its original formulation these included contrast, density, and blur of the image contours. More recent studies have added several other visual characteristics that increase the stimulus strength, such as motion (Blake, Zimba, & Williams, 1985; Bossink, Stalmeier, & de Weert, 1993; Wade, De Weert, & Swanston, 1984), spatial frequency (Arnold, Grove, & Wallis, 2007; Fahle, 1982), color contrast (Bossink et al., 1993), and overall luminance (O'Shea, Blake, & Wolfe, 1994). In addition to the strength of the rivaling stimuli, binocular rivalry is also affected by secondary visual factors. One example is the visual context of the rivaling stimuli. If the rivaling stimuli are surrounded by a certain visual context, dominance tends to increase for the stimulus that is congruent with that context (Blake & Logothetis, 2002; Sobel & Blake, 2002). In addition to visual context, the familiarity of a stimulus can also increase its dominance, as is the case for upright faces versus inverted faces (G. Zhou, Zhang, Liu, Yang, & Qu, 2010), for recognizable figures versus unrecognizable figures (Yu & Blake, 1992), and for words versus non-words (Wolf & Hochstein, 2011).

The most obvious measure of binocular rivalry is the percentage of time a stimulus is dominant, i.e. overall dominance. When an experimental manipulation causes the overall dominance of a stimulus to increase, this can be mediated by prolonged dominance durations or by shortened suppression durations. These two temporal characteristics are independent of one another, they depend on distinct neural mechanisms, and they are affected differently by different experimental manipulations (Blake & Logothetis, 2002). For example, increasing the stimulus strength of one of the stimuli has an asymmetrical effect. Perhaps counterintuitively, it mainly shortens the average suppression duration of that stimulus, and increases dominance durations only little, if at all (Bossink et al., 1993; Brascamp, Klink, & Levelt, 2015; Levelt,

1965; Mueller & Blake, 1989). The fact that increasing the strength of one stimulus, leads to shorter percepts of the other stimulus can be explained by reciprocal inhibition models of binocular rivalry (Tong et al., 2006). Apart from dominance and suppression durations, a third temporal characteristic of binocular rivalry is the overall switch rate. This is a measure of the combined perceptual stability of both stimuli. Increasing the strength of both rival stimuli to a similar degree causes the overall switch rate to increase robustly (Brascamp et al., 2015; Levelt, 1965).

As mentioned before, voluntary control during binocular rivalry is very limited. Voluntary (endogenous) attention can slightly increase dominance durations of the attended stimulus, but it leaves its suppression durations unaffected (Ooi & He, 1999; Paffen & Alais, 2011). Thus, the effect of attention on the temporal characteristics of binocular rivalry follows the reverse pattern of that of stimulus strength. This should not be surprising, since attending to something that is not visible is paradoxical. Involuntary (exogenous) attention on the other hand can also shorten suppression durations, but it does so mainly by making a perceptual switch more likely in general (Ooi & He, 1999). Another interesting effect is that withdrawing attention from both rivaling stimuli, by increasing irrelevant task demands, slows down the switch rate of binocular rivalry (Paffen, Alais, & Verstraten, 2006). However, it does not stop perceptual switches completely, no matter how distracted a participant is, which shows that attention is certainly not necessary for binocular rivalry to occur (Paffen & Alais, 2011).

1.3.2 Cross-modal effects in binocular rivalry

Recently, various cross-modal effects on binocular rivalry have been demonstrated. For each of these effects, nonvisual sensory stimulation increases the overall dominance of a congruent visual stimulus. Based on the effects of stimulus strength and attention described above, an important dissociation needs to be made between cross-modal effects that merely increase the dominance duration of the congruent visual stimulus, and those that shorten suppression durations as well. In the first report of such a cross-modal effect on binocular rivalry, looming sounds increased the dominance duration of a looming visual stimulus but suppression durations remained unaffected (van Ee, van Boxtel, Parker, & Alais, 2009). This effect was amplified by tactile stimulation from the vibrating speaker (van Ee et al., 2009). Thus, looming sounds only had an effect during visual awareness of the congruent stimulus, and therefore voluntary attention could potentially explain the result. In fact, such a mediating role of attention was specifically tested. Participants were instructed to perceive the looming stimulus as much as possible. The co-occurrence of the looming sound increased the effect of voluntary attention. However, no change was found when participants were instructed to perceive the incongruent rivaling stimulus as much as possible. Similar audiovisual interactions have been described for directional sounds with moving visual stimuli (Conrad, Bartels, Kleiner, & Noppeney, 2010), melodic sounds with written musical notes (Lee, Blake, Kim, & Kim, 2015), and the sound of syllables with the congruent motion of lips (Vidal & Barrès, 2014). In each of these studies, the increased overall dominance was due to

prolonged dominance without shortened suppression. Therefore, the effects can (partly) be explained by top-down attention.

However, nonvisual sensory stimulation has also been shown to decrease suppression durations of congruent visual stimuli (often in combination with prolonged dominance durations). Such a pattern of results is similar to the effect of increased stimulus strength. The most elaborate description of such a cross-modal effect is that of touch. During binocular rivalry between orthogonally oriented visual gratings (as in Figure 4), the active exploration of a haptic gradient increases the overall dominance of the congruent visual stimulus, by elongating dominance and shortening suppression (Lunghi, Binda, & Morrone, 2010). These effects only occur when the spatial frequency of the gratings (Lunghi et al., 2010) as well as their orientation (Lunghi & Alais, 2013) are congruent. Interestingly, placing the haptic grating away from the perceived location of the visual grating abolishes the effect (Lunghi & Morrone, 2013). This suggests that the haptic gradient and the visual stimulus need to be perceived as one and the same object, i.e. that they follow the spatial rule of multisensory integration. In a follow-up study, it was found that the depth of suppression was truly reduced by the congruent haptic stimulus, instead of the haptic stimulus merely weakening the stability of the incongruent rivaling stimulus (Lunghi & Alais, 2015). In addition to this visuotactile interaction, the shortening of suppressions has been found for a moving stimulus that is congruent with active hand movements (Maruya, Yang, & Blake, 2007), for a visual stimulus that is congruent with olfactory stimulation (the image of a rose and the smell of a rose; Zhou, Jiang, He, & Chen, 2010), and for a visual stimulus that is congruent with ecologically relevant sounds (the image of a bird and the sound of a birdsong; Chen, Yeh, & Spence, 2011). Such rescue of a visual stimulus from suppression through cross-modal interactions has been hypothesized to be indicative of multisensory awareness (Deroy et al., 2016). According to this hypothesis, the observed visual grating and the felt haptic grating mentioned above are perceived as one and the same object through multisensory integration. The multisensory awareness of that object would then effectively increase the visual stimulus strength of that object.

Now, let us return to body-ownership. As described in section 1.1, body-ownership is essentially caused by multisensory integration of vision, touch, and proprioception (Ehrsson, 2012). It is a clear example of multisensory awareness, albeit more special than that of an external object. For one, it incorporates all possible senses, including proprioception. Furthermore, our body is the most relevant object there is – it is who we are. We move it around to accomplish our goals, and we need to defend it against threats. Therefore, it seems logical that visual awareness of our body would be prioritized. To put it differently, body-ownership should boost the visual awareness of our body. Study III combines binocular rivalry with the rubber-hand illusion to test this novel hypothesis, thereby building on the existing knowledge of binocular rivalry, including the roles of attention and stimulus strength. We predict that if one of the rivaling stimuli during binocular rivalry is the image of a hand for which ownership is experienced, the stimulus strength of that image should be greater, compared to when no ownership is perceived for that same hand.

1.3.3 Continuous flash suppression

Another method to study visual awareness is continuous flash suppression (CFS). During CFS one eye is presented with a flickering high-contrast stimulus (i.e. the mask), while the other eye receives a visual stimulus of interest. It could be interpreted as a special case of binocular rivalry, in which the stimulus-strength of the mask is so great that it prevents the other visual stimulus from reaching awareness for long periods of time. Not only does CFS induce very long suppression durations, the suppression is also much deeper than that in traditional binocular rivalry (Tsuchiya, Koch, Gilroy, & Blake, 2006).

Which aspects of a visual stimulus hasten a break through suppression? This question is rather similar to the question of what decreases the suppression duration during binocular rivalry. However, a crucial difference is that participants are not aware of the content of the suppressed visual stimulus. Thus, confounding factors that might play a role in binocular rivalry, such as attention, memory, and response bias are abolished. Unsurprisingly, the stimulus strength of the suppressed stimulus affects the speed with which it is rescued from suppression (Tsuchiya & Koch, 2005; Yang et al., 2012). And similar to what had been described for binocular rivalry, it is affected by the familiarity of the visual stimulus. Upright faces (Jiang, Costello, & He, 2007) and upright bodies and body parts (Stein, Sterzer, & Peelen, 2012) are detected faster then when these stimuli are upside down. And finally, cross-modal effects have been described. Moving lips are recovered from suppression faster when they are accompanied by congruent speech (Alsius & Munhall, 2013), which is indicative of an audiovisual interaction. And the orientation of a hand image that is congruent with the orientation of an observer's hand speeds the recovery of that image from suppression (Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013), suggesting a facilitating effect of proprioception. Other effects on the suppression duration during CFS include that of priming and working memory (for a review, see Gayet, van der Stigchel, & Paffen, 2014).

In line with its hypothesized effect on binocular rivalry, we predicted that body-ownership would decrease the time needed for a hand image to break through suppression. But how can ownership be experienced for a hand that is not consciously seen? Would it be possible to use visuotactile stimulation to induce a rubber hand illusion during CFS, i.e. without visual awareness of the hand and the touches applied to it? A suppressed stimulus in CFS is processed outside of awareness and can affect conscious perception and other cognitive functions in a large variety of ways (for a review, see Yang, Brascamp, Kang, & Blake, 2014). The provocative idea that it might be possible to induce unconscious ownership originates from three main observations, two of which consist of visual information that needs to be processed in the absence of awareness. First, the brain would need to know that the image of a hand is hidden behind the mask, and that this hand is oriented in such a way that it could be part of the body. Second, it would need to process the movement of the masked object that is touching the masked hand. Indeed, both the orientation of a hand image (Salomon et al., 2013) and the motion of a stimulus (e.g. Itoh, Fujii, Kwee, & Nakada, 2005; Koivisto, Mäntylä, & Silvanto, 2010; Maruya, Watanabe, & Watanabe, 2008) are processed in the absence of visual awareness. A third necessity for unconscious ownership would be

multisensory integration of the unconscious visual stimulus with the tactile stimulus. Evidence for such integration is derived from Study III and from the studies of Lunghi and colleagues (2010, 2013, 2015) in which a tactile stimulus shortens the suppression duration of a visual stimulus. In fact, multisensory integration (audiovisual) can occur in the absence of awareness of both sensory modalities (Faivre et al., 2014). Thus, the requirements for an unconscious version of the rubber hand illusion seem present, and in Study IV we provide evidence for such an effect. Subsequently, we use this unconscious rubber hand illusion to assess the effect of unconscious ownership on the recovery from suppression.

2 AIMS

The general aim of this thesis was to investigate the relationship between body-ownership and visual perception. More specifically, we sought to determine the effect of body-ownership on two fundamental aspects of visual perception: visuospatial perception and visual awareness, and to assess the necessity of (visual) awareness in body-ownership.

- The aim of Study I was to examine the relative contribution of different potential mechanisms by which body-ownership could affect the perceived size of objects in the own-body-size effect.

- The aim of Study II was to investigate the mechanism by which body-ownership initiates a rescaling of external space in the own-body-size effect.

- The aim of Study III was to investigate the effect of body-ownership on visual awareness of one's own body.

- The aim of Study IV was to examine the possibility of body-ownership in the absence of awareness, and to investigate the effect of such unconcious ownership on visual suppression.

3 METHODS

3.1 PARTICIPANTS

All participants (n = 245) were recruited from the Stockholm student population. They had normal vision, or corrected to normal vision with contact lenses. Wearing glasses was not possible because of the physical restrictions of the head mounted displays. Participants gave their written informed consent prior to the experiment, and importantly all were naïve to the purpose of the studies. Experiments were approved by the Regional Ethical Review Board of Stockholm and were in accordance with the declaration of Helsinki.

3.2 HEAD-MOUNTED DISPLAYS

In each experiment, visual stimuli were presented through a set of head-mounted displays (HMDs). The choice of HMDs was an important step in designing the experiments, since each of them have their advantages and disadvantages. Selecting the right HMDs for an experiment was based on the purpose of that particular experiment, and often required piloting. We used three different HMDs. In Study I we used the CybermindVisette Pro PAL (Cybermind Interactive, Maastricht, the Netherlands; display resolution = 640 × 480, diagonal field of view = 71.5°). The advantage of this system is its relatively wide field of view, while its drawback is its low resolution. Because Study I investigates visuospatial perception, a wider field of view is preferred over a higher spatial resolution. In Study II we used the Oculus Rift HMDs (Oculus VR, Menlo Park, California, United States; display resolution = 1920 x 1080, diagonal field of view = 110°), which has a higher display resolution as well as a wider field of view than the CybermindVisette Pro PAL, but was not available at the time of Study I. Another advantage of the Oculus Rift HMDs is that they allow for the playback of videos, which was necessary in Study II, whereas the CybermindVisette Pro PAL only allows for a live display of the input of two cameras. In Study III and Study IV we used the VR1280 (Virtual Realities LLC, League City, Texas, United States; display resolution = 1280 x 1024, diagonal field of view = 60°). Despite a lower resolution than the Oculus Rift, its effective resolution per degree of visual field is higher due to its narrow field of view. Since Study III and Study IV did not require a wide field of view, the VR1280 was preferred. The VR1280 allows for the playback of videos as well, which was a necessity for Study III and Study IV. Another big advantage of the VR1280 is the ability to manually adjust the distance between the two displays, so as to match participants' individual inter-ocular distance. The one major disadvantage of the VR1280 is their lack of comfort compared to the Oculus Rift, which becomes noticeable during the course of a typical experiment (30 – 60 minutes).

3.3 VISUAL AND TACTILE STIMULI

Acquiring optimal visual stimuli can be a timely process that relies on the creation and piloting of many different stimuli versions to assess their effectivity. The following sections give an overview of the visual stimuli that were used in the different studies, as well as some considerations that led to the choice of these stimuli.

3.3.1 Stimuli of Study I

In Study I, the HMDs displayed the real-time input from two cameras (Protos IV, Vista, Workingham, Berkshire, United Kingdom) that were mounted to a tripod. The height of the tripod was identical for different conditions in order to match for visual cues, such as linear perspective and the height-on-a-plane of target objects. The cameras were facing down a small artificial body (80 cm) or a large artificial body (400 cm), rendering a three-dimensional first-person perspective of those bodies. Cameras were tilted in such a way that the bodies were visible from the waist down, i.e. the chest was not visible, so as to maximize the visible portion of the testing room, which included a door, a desk, and a chair. These visible objects could have functioned as a familiar size cue against our hypothesized effect, but were included to increase the ecological validity of our experiments. During visuotactile stimulation, participants could see a small ball attached to a stick (hereafter referred to as 'tactile probe') stroking the lower legs and feet of the artificial body (Figure 5A,D). The size of the tactile probe and the length of the strokes were proportional to the size of the artificial body. In the *synchronous conditions*, participants' veridical body and the artificial body were touched synchronously and spatially congruent at corresponding body-parts. In the

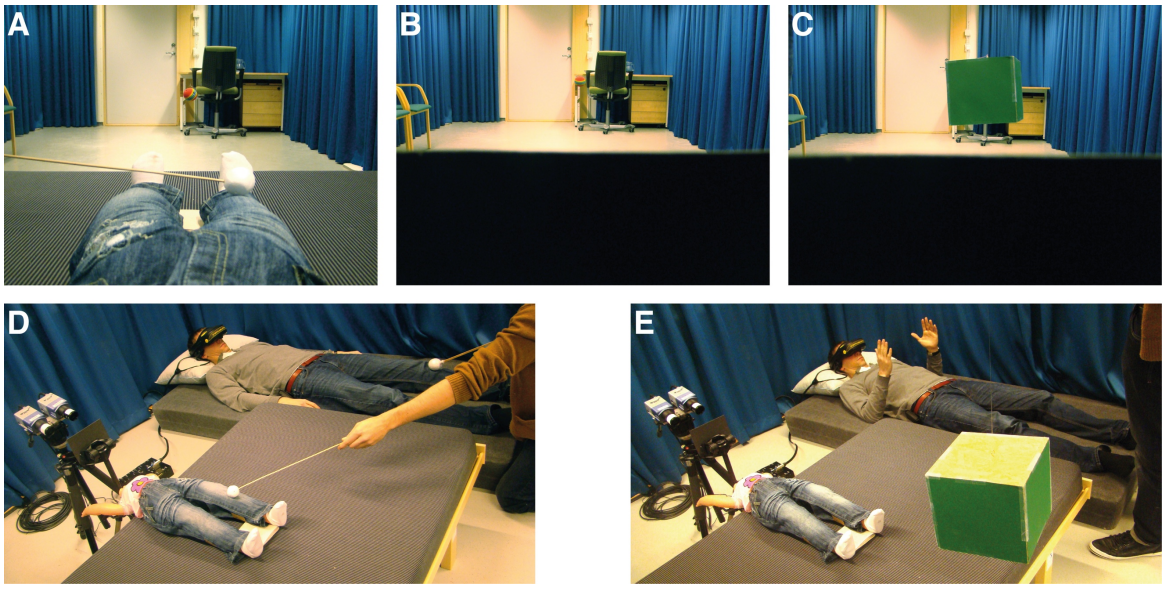

Figure 5. Visual stimuli (**A-C**) and experimental setup (**D,E**) of Study I. Visuotactile stimulation phase (**A**), occlusion of the upper half of the visual field (**B**), and target object presentation (**C**). Synchronous visuotactile stimulation (**D**) and object size estimation (**E**). Small red ball (**A,B**) is participants' fixation point in Experiment 2.

asynchronous conditions these touches were asynchronous and applied to non-corresponding body-parts (but matched in terms of overall tactile stimulation, i.e. the two lower legs and feet). The reason for violating both the temporal rule (synchronicity) and the spatial rule (spatial congruence) in the asynchronous conditions was to maximize the disruption of ownership. After one minute of visuotactile stimulation, the lower half of the visual field, in which the artificial body was located, was occluded (Figure 5B). A few seconds later, a target object (10 cm, 20 cm, or 30 cm) appeared in the upper half of the visual field at 1.2 m from the cameras (Figure 5C,E). The occlusion was removed before the start of the next trial. The visual stimuli of Experiment 2 were identical to those of Experiment 1, except for the addition of a fixation ball that was hanging from a fishing line at a fixed distance (1.5 m) in each condition. This distance was close enough to either body to prevent those bodies from appearing blurry, whilst still being behind the location of target objects. As a result, upon target object presentation, the fixation ball was occluded and fixation was automatically moved to the target object. In Experiment 3, target objects appear either *near* (1.0 m) or *far* (6.0 m) from the cameras.

3.3.2 Stimuli of Study II

Study II used prerecorded videos instead of a real-time display as in Study I. Videos were recorded with two cameras (CamOne Infinity, CamOneTec, Delbrück, Germany), and processed using Final Cut Pro X (Apple Inc., Cupertino, United States). In the videos, an empty room was visible, with a bed in the foreground in the small-body conditions (Figure 6). A brush would enter the field of view at regular intervals, brushing in empty space at four different locations, matching both lower legs and both feet of either a small (80 cm; Figure 6A) or a large (400 cm; Figure 6C) invisible body. The videos contained an audio-track that

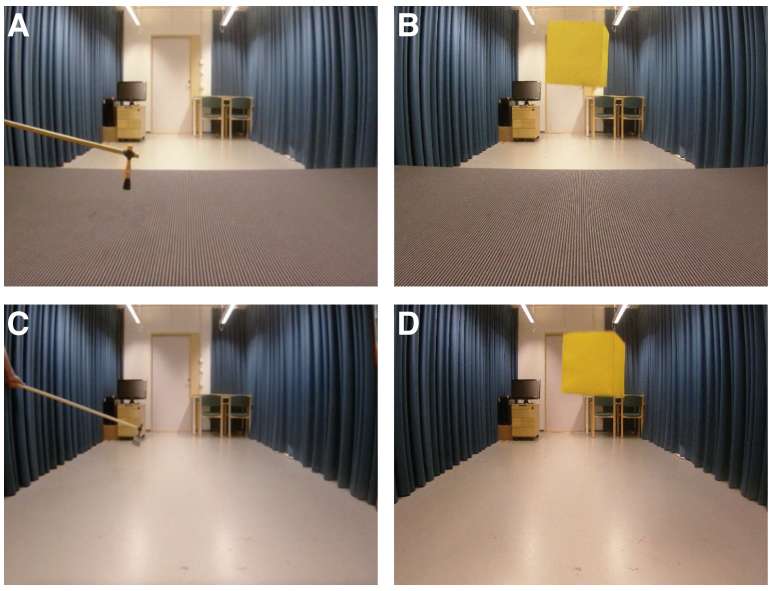

Figure 6. Visual stimuli of Study II. Visuotactile stimulation phase (**A**) and target object presentation (**B**) during small invisible body conditions, and during large invisible body conditions (**C,D**).

was only audible to the experimenter, which was used to synchronize tactile stimulation with the visual appearance of touch as seen in the videos. We used pre-recorded videos in Study II because it was not possible to reliably touch the correct parts of empty space without having a body to guide the brush movement. Again, tactile stimulation of participants' veridical body was either synchronous or asynchronous with the observed touches. After one minute of visuotactile stimulation, a target object appeared at 1.5 m from the cameras (Figure 6B,D).

3.3.3 Stimuli of Study III

In Study III, the HMDs were not used for stereoscopic vision, but to induce binocular rivalry. Binocular rivalry stimuli were created using Final Cut Pro X. One eye was presented with the image of a hand on a red background (Figure 7). The hand image was generated using a photo of a hand on top of a green screen, which allowed for isolation of the hand. The red colors of this image were enhanced, without the hand appearing unnatural, in order to maximize the color contrast between the two rivaling images, and thereby decrease piecemeal rivalry (see section 3.6). The other eye was presented with randomly generated Mondrian masks consisting of different sized rectangles in different shades of blue. A new Mondrian mask appeared every 0.1 s (10 Hz). Three layers were added on top of each of these rivaling stimuli, and were therefore visible at all times. Both stimuli were surrounded by a white circle, and both stimuli contained a fixation cross in the middle of the stimulus. In addition, both stimuli contained a moving tactile probe, i.e. a small ball on a stick. The moving tactile probe layer was created by covering the same hand that was used for the hand stimulus with a green screen and recording a video of the tactile probe approaching the hand from the side, stroking it from the back of the hand to the tip of the index finger, and then withdrawing from the hand to the starting position. Using the green screen this way, allowed for the isolation of this visual layer and its addition to both rivaling stimuli. If the moving tactile probe would only be present in the hand stimulus, it would greatly increase the relative strength of that stimulus, such that the hand would be dominant almost continuously. Tactile stimulation was applied to participant's veridical hand synchronous to the movement of the tactile probe by listening to an audio track.

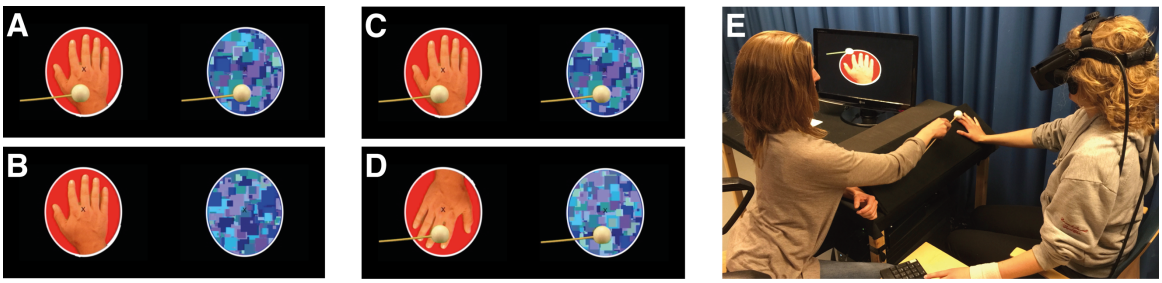

Figure 7. Visual stimuli (**A-D**) and experimental setup (**E**) of Study III. Visuotactile and visual-only conditions (**A**), and tactile-only and no-stimulation conditions (**B**) of Experiment 1. Congruent visuotactile and visual-only conditions (**C**) and incongruent visuotactile and visual-only conditions (**D**) of Experiment 2. Panel **E** displays the experimental setup during a congruent visuotactile trial.

3.3.4 Stimuli of Study IV

In Study IV, we used the same HMDs as in Study III, but this time for the purpose of continuous flash suppression (CFS). One eye was presented with the same Mondrian masks that were used in Study III. This masking stimulus was identical in each of eleven videos that were created for Experiment 1a and Experiment 2. The other stimulus consisted of the same hand image as used in Study III, but with a black background instead of a red background (Figure 8). In addition, the brightness of the hand was lowered to 50% of the original brightness, which was the maximum brightness used in this study. In one video, the brightness of the hand increased linearly from 0% to 50% in 240 seconds. This video was used in Experiment 1a to assess the brightness at which the hand would break through suppression for an individual participant. Subsequently, one of ten videos would be selected based on the highest hand brightness that was suppressed. In these ten videos, the brightness of the hand was fixed, ranging from 2.5% to 25% (in 2.5% increments) of the original brightness (Figure 8A,B). In Experiment 1b, the Mondrian mask was removed, while the hand was at 50% brightness (Figure 8C,D). And in Experiment 2, the video from Experiment 1a was used in which brightness increased linearly over time (Figure 8E,F). The tactile probe layer used in Study III, was made entirely black in order for it to disappear in the black background when it was not stroking the hand, and for it not to be visible next to the circular stimuli. Importantly, in Study IV, the tactile probe layer was only added to the hand image. This was done in order to prevent the possibility of participants experiencing an invisible hand illusion during dominance of the mask (Guterstam et al., 2013). A white fixation cross was present in the middle of each stimulus. Again, tactile stimulation was cued through an audio track listened to by the experimenter, which consisted of strokes from the back of the hand to the tip of the index finger.

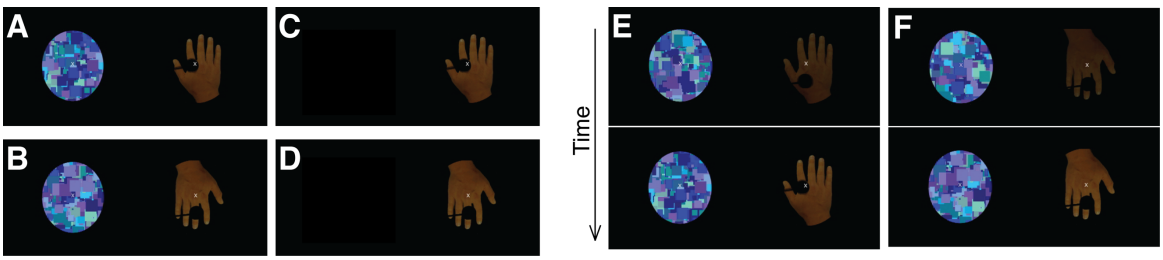

Figure 8. Visual stimuli of Study IV. Congruent condition (**A**) and incongruent condition (**B**) of Experiment 1a, and of Experiment 1b (**C,D**). Congruent condition (**E**) and incongruent condition (**F**) of Experiment 2 in which the brightness of the hand image increases over time.

3.4 MEASURING OWNERSHIP

In Studies I-III, the manipulation of body-ownership is used as a method to investigate its effect on visual perception, whereas in Study IV, body-ownership is the primary dependent variable of interest. However, to confirm its successful manipulation, body-ownership was still measured in the first three studies. The measure of choice was subjective report of ownership on a standardized questionnaire. At the end of the main part of the experiment, on a separate trial, participants rated different statements on a seven-point Likert-scale ranging from -3 to +3, where -3 indicates "strongly disagree", 0 indicates "do not agree, do not disagree", and +3 indicates "strongly agree". The exact formulation depended on the details of the experiment, i.e. whether the experiment used a full-body illusion (Study I), an invisible body illusion (Study II), or a hand-ownership illusion (Study III and IV). However, all questionnaires had in common that they included ownership statements to capture the experience of ownership (e.g. "It felt as if the body I saw was my body"), and control statements to capture expectancy effects and task compliance effects (e.g. "It felt as if I had two bodies at the same time"). The difference between the mean ratings of illusion statements and the mean ratings of control statements was calculated as a measure of the *illusion strength*. The success of ownership manipulation was assessed by statistically comparing the illusion strength between conditions of interest. And in order to gain more insight into different aspects of the illusion, the median rating on single illusion statements was statistically compared between conditions. Apart from confirming a successful manipulation of ownership, the ownership questionnaire also allowed for the statistical testing of possible inter-individual correlations between ownership and its effect on visual perception. Such correlations are suggestive of a direct link between ownership and visual perception, and could therefore support the conclusions drawn from the main results.

3.5 MEASURING SIZE PERCEPTION

Each experiment in Study I and Study II measured size perception in four conditions in which body-size and visuotactile synchrony were manipulated in a 2x2 full factorial design: small-synchronous, small-asynchronous, large-synchronous, and large-asynchronous. Two different measures of size perception were used: bimanual estimation and verbal report (similar to van der Hoort et al., 2011). For bimanual estimations, participants were instructed to indicate the perceived size of a target object by holding their two hands in front of them (Figure 5E), while the experimenter measured the distance between the palms of their hands. A tap on the back of their hand was used to communicate to the participant that they could lower their hands. In Experiment 1b of Study I we used verbal report, in which participants were instructed to verbally estimate the size of target objects "as quickly and accurately as possible". A significant drawback of verbal report is that participants are much more inaccurate and inconsistent, as compared to bimanual estimation. Verbal report can be interpreted as a more explicit measure, whereas bimanual estimations are more implicit. Furthermore, since bimanual estimation is an action-based measure of object size, whereas

verbal report is not, the two measures might rely on different visual processing streams in the brain. Bimanual report would depend more on the dorsal stream, which processes 'vision for action', whereas verbal report would depend more on the ventral stream, which processes 'vision for perception'. Naïve participants were recruited for each experiment, and therefore, the data presented in this thesis do not allow for a correlation between these two measures.

A crucial aspect of measuring size perception in Study I and Study II, is that all statistical comparisons were carried out within participants, since the variability between participants could overshadow the effects of our experimental manipulations. Therefore, each participant was included in each condition, and analyses were performed on normalized differences between those conditions, i.e. the difference between conditions was divided by individual averages. The reason for normalization is that, in addition to decreasing random inter-subject variability, it provides a better measure of changes in perception. For example, perceiving an object as 10 cm during the small-body illusion, and as 5 cm during the large-body illusion, is phenomenological analogue to a change from 40 cm to 20 cm, and therefore these outcomes should be weighted equally. Taking the mere difference between conditions ($10 - 5 = 5$; and $40 - 20 = 20$) does not account for the similarity of these perceptual changes.

3.6 MEASURING VISUAL AWARENESS

In Study III we used binocular rivalry to measure visual awareness. Experiment 1 consisted of four conditions in a 2x2 full-factorial design in which the visual and tactile component of touch (touch of the hand in the image and touch of participant's veridical hand) were either present or absent: visuotactile, visual-only, tactile-only, and no-stimulation (Figure 7A,B). In addition, we included a baseline condition that was identical to the no-stimulation condition, but with participants' veridical right hand folded back to their left abdomen. Comparing this baseline condition to the no-stimulation condition would show the possible influence of visuoproprioceptive congruence *per se*. Experiment 2 also consisted of four conditions in a 2x2 full-factorial design, but here we manipulated the orientation of the hand (right-side up/congruent or inverted/incongruent), and the tactile stimulation of participants' veridical hand. The moving tactile probe was visible in each condition because Experiment 1 had shown a large effect of this moving object on dominance, rendering the visual-only condition as the most appropriate baseline. The four conditions were: congruent visuotactile, congruent visual-only, incongruent visuotactile, and incongruent visual-only (Figure 7C,D).

Participants in Study III were instructed to fixate on the fixation cross at all times. During a test trial, participants could manually adjust the distance between the two displays to match their individual inter-ocular distance, after which the distance was fixed for the remainder of the experiment. In both experiments, participants were naïve to binocular rivalry, and therefore the test trial was also used to familiarize participants with the phenomenon. Although testing naïve participants is not standard in binocular rivalry research, the need for

participants to be naïve to the rubber hand illusion excluded participation of most people in the department. Participants were required to be naïve to the rubber hand illusion to prevent expectancy effects from confounding the results. Importantly, the binocular rivalry data that was used for analysis was gathered before a separate trial tested participants' subjective experience of ownership.

Participants' right hand was placed on a custom-made titled platform in such a way that their hand would be in the same retinal location as the hand image if they were to take of the HMDs (Figure 7E). Therefore, there was no visuoproprioceptive incongruence to be resolved by the rubber hand illusion. Participants were instructed to press and hold a button, indicating which of the two stimuli was most dominant at any given time. When a patchwork of the two images was perceived (i.e. piecemeal rivalry), participants responded as to which image was the most dominant. In general, piecemeal rivalry is an unwanted phenomenon, especially when the contribution of both images gets close 50/50, because it is more difficult for participants to assess the dominant percept, and therefore it may be more prone to response biases. Visual stimuli of larger retinal size are more likely to result in piecemeal rivalry, especially during the transition between two dominant percepts. The largest retinal size of simple stimuli, such as orthogonal line elements, that prevents piecemeal rivalry altogether is 1.0 degree (Blake, O'Shae & Muller, 1992). However, for more complex stimuli such as faces this maximum retinal size is much larger (6.0 degrees) (Alais & Melcher, 2007). Given that the average retinal size of a hand is approximately 10 degrees when the arm is stretched, a trade-off had to be made between the hand being realistically large enough to be embodied but not so large as to induce too much piecemeal rivalry. Based on pilots with different sized stimuli, the optimal trade-off appeared to be a stimulus size of 10 degrees, with the hand being 8.5 degrees.

Experiment 2 of Study III used an inverted hand as a control condition, in which ownership for the hand would not be induced, despite synchronous visuotactile stimulation, because of the incongruence between vision and proprioception. Another way to abolish ownership is to apply asynchronous visuotactile stimulation, such as in Study I and Study II. There are several reasons why asynchronous visuotactile stimulation was not preferred in this experiment. First, the control condition was supposed to disentangle the effect of ownership from synchronous visuotactile stimulation *per se*. Second, since asynchronous stimulation does not lead to multisensory integration, it would effectively double the amount of perceived sensory events, and this could have unanticipated effects that are difficult to interpret. And third, asynchronous stimulation might be a source of exogenous attention related to error-monitoring, which could affect dominance durations (see 1.3.1) but this would relate to a different research question.

3.7 MEASURING UNCONSCIOUS OWNERSHIP

In Experiment 1a of Study IV we aimed at developing a rubber hand illusion in the absence of visual awareness of that hand (i.e. the unconscious rubber hand illusion), by applying continuous flash suppression (CFS) to the hand image. We compared two conditions with identical synchronous visuotactile stimulation, but with the hand-image oriented right-side up or inverted, i.e. congruent or incongruent.

As described in section 3.3.4, the first part of the experiment was to assess participants' individual threshold for the hand image brightness that could be suppressed. In the second part of the experiment, participants fixated on the fixation cross while they received tactile stimulation of their hand. Two measures of body-ownership that are well described in body-ownership research were used: skin conductance response (SCR) to a knife threat and proprioceptive drift (see section 1.1.1). Because we wanted to measure proprioceptive drift, the participants' right hand was not placed at the exact location of the hand image as in Study III, but instead it was placed 20 cm to the right. To ensure that participants would not rotate their head towards their hand, they had their chin placed on a chin-rest, restricting such movement. To measure the SCRs, two electrodes were attached, one to the index finger of the left hand and one to the middle finger of the left hand. After one minute of tactile stimulation, a knife would appear to stab the masked hand on 50% of the trials. This knife was present in both the mask-stimulus and the hand-stimulus, rendering it clearly visible to the participant. The other half of the trials were used to measure proprioceptive drift. Before the start of every trial, participants' left index finger was placed on a vertical metal bar that hung over the table on which participants' right hand was placed. Participants were to slide their finger towards the perceived location of their right index finger. The reason for performing this hand localization task at the onset of each trial was to keep participants naïve as to whether the knife would appear or not. If the knife did not appear at the end of a trial, a second hand localization task would be performed to complete the proprioceptive drift measure (defined as the difference between the two hand localization tasks).

Experiment 1b was identical to Experiment 1a, except for the stimuli used (see 3.3.4), and without the assessment of individual brightness thresholds at the start of the experiment. Instead, in Experiment 1b, an additional trial was included for both conditions at the end of the experiment after which participants filled in an ownership questionnaire.

Experiment 2 was designed to test the prediction that unconscious ownership would hasten the break through suppression of the hand-image. To this end, we used the video of Experiment 1a in which the brightness of the hand linearly increased over time. Participants' hand was synchronously touched with touches applied to the masked hand. Crucially, in contrast to Study III and as described in 3.3.4, the moving tactile probe that touched the hand in the image was masked as well. Participants pressed one of two buttons to indicate the orientations of the hand as quickly as possible.

4 OVERVIEW OF STUDIES

4.1 STUDY I

The own-body-size effect on visuospatial perception as described in van der Hoort, Guterstam and Ehrsson (2011) states that the perceived size and distance of objects is inversely related to the body size of an observer. In the small-body illusion objects appear larger and further away, and *vice versa*, in the large-body-illusion objects appear smaller and closer by. The presence of body-ownership was shown to maximize this effect. We hypothesized that body-size rescales the entire spatial layout of external space, independent of visual cues. Indeed, experiments in the original publication of the own-body-size effect (van der Hoort et al., 2011), controlled for most visual cues. The distance of target objects from the cameras remained the same in each condition, thus the retinal size of target objects in these conditions was identical. Additionally, regarding the remaining visual information, all but the size of the artificial body was identical across conditions. Thus, pictorial cues, such as occlusion, texture gradient, or linear perspective could not explain the own-body-size effect. And since neither the participants nor the cameras moved, motion based visual cues could not have played a role either. However, despite the fact that the original publication of the own-body-size effect controlled for most visual cues, we identified two possible mechanisms by which visual cues could have contributed to the effect.

Firstly, body-ownership could enhance the contribution of the visible body as a *familiar size cue*. The idea here is that observing a body from the natural first-person-perspective would be a very important cue for the size and distance of other objects. In the presence of ownership, i.e. when it is your own body that you are observing, the contribution of this familiar size cue could be greater. Therefore, in Experiments 1a and 1b we assessed the contribution of the body as a familiar size cue by occluding the body after induction of the full-body illusion but before the presentation of target objects (Figure 9A-B). We found that occluding the body did not abolish the own-body-size effect, and therefore, the body as a familiar size cue cannot explain the effect of ownership on visual perception. Interestingly, in the asynchronous control conditions of Experiment 1a and 1b, objects were perceived as being of equal size, unaffected by whether participants had seen a small body or a large body before target objects appeared. This is different from the initial report on the own-body-size effect, in which a small effect was described for the asynchronous conditions as well. Thus, the body-size effect in the absence of ownership seems to be caused by the visible body being used as a familiar size cue, which is effectively prevented when the body is occluded.

A second possibility is that body-ownership could enhance the contribution of *oculomotor cues*. In van der Hoort et al. (2011), when a target object entered the field of view, participants moved their fixation from the body to the object. Since the distance between target objects and the cameras was constant, participants' fixation changed differently in the small-body illusion and the large-body illusion. In the small-body illusion, participants' eyes had to diverge in order to move fixation from the body towards target objects, whereas in the large-

body illusion, participants' eyes had to converge. Similarly, accommodation of the eyes' lenses changed differently in the two body-size conditions. If the contribution of these oculomotor cues were to be larger in the presence of ownership, because they are more informative when the own body is involved, they could explain the own-body-size effect. Therefore, in Experiment 2, we controlled for these oculomotor cues by having participants fixate on a fixation point during the induction of the full-body illusion. The location of this fixation point was identical for all conditions, and therefore changes in eye-vergence and accommodation were identical. In addition, this procedure controlled for possible attentional differences between ownership and no-ownership conditions. Experiment 2 resulted in an own-body-size effect of similar size as that in Experiment 1a, and similar to Experiment 1a, asynchronous stimulation completely abolished the effect (Figure 9C). Thus, oculomotor cues do not seem to play a role in the own-body-size effect. We also included an ownership questionnaire on a separate trial after the size estimation trials and found that the stronger participants experienced the illusion, the stronger their own-body-size effect was.

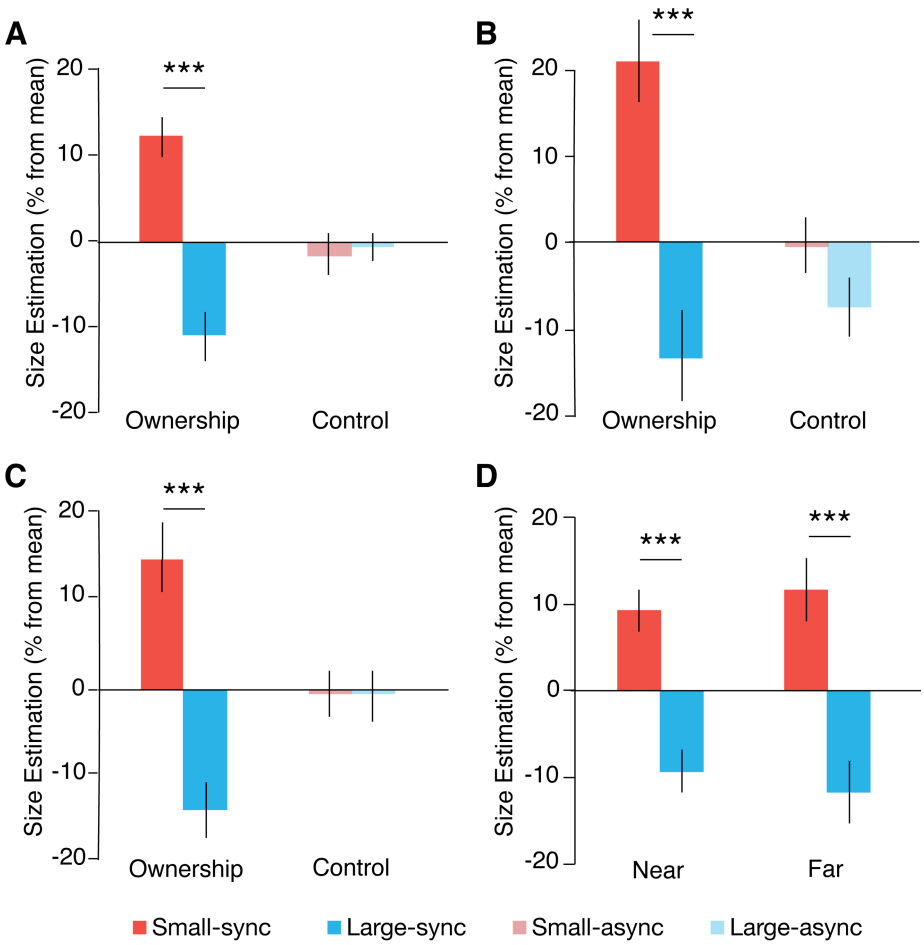

Figure 9 Main results of Study I. Bimanual size estimations in Experiment 1a (**A**), verbal size estimations in Experiment 1b (**B**), and bimanual size estimations in Experiment 2 (**C**) and Experiment 3 (**D**), as a percentage deviation from individual means. Small/Large = small and large artificial bodies; synchronous/asynchronous = synchronous and asynchronous visuotactile stimulation. ***p < 0.001.

The combined results of Study I and the original publication (van der Hoort et al., 2011) indicate that, *during* object size perception, the effect of body size depends on two independent additive mechanisms. The body that is seen from the natural first-person perspective can act as a familiar size cue. This effect is independent of ownership since disrupting ownership through asynchronous visuotactile stimulation does not entirely abolish it (van der Hoort et al., 2011). Additionally, body-ownership of a different sized body causes a recalibration of external space, which leads to changes in object size perception. This effect is independent of visual cues since occluding the body, and controlling for fixation does not terminate the recalibration (Study I).

An additional aim of Study I was to assess the spatial extent to which such recalibration applies. The space that surrounds our body and in which we can directly act, i.e. *peripersonal space*, is represented differently from space that is further away (Fogassi et al., 1996; Holmes & Spence, 2004; Makin, Holmes, & Zohary, 2007; Tamar R. Makin, Holmes, & Ehrsson, 2008). It could be argued that scaling visual space to body-size is especially useful for objects that we can immediately act upon, and therefore that the own-body-size effect might be greater in peripersonal space. In contrast, if the own-body-size effect reflects a true recalibration of external visual space, there should be no difference between different parts of space. To distinguish between these two alternatives, we compared the own-body-size effect close to the body (1 m from the cameras) and far from the body (6 m from the cameras). The results of Experiment 3 show that the own-body-size effect does not reduce with increased distance of target objects (Figure 9D). Thus, the visual recalibration is not specific for peripersonal space, but instead affects visual space equally at different distances.

4.2 STUDY II

Study I showed that once the full-body illusion is induced, visibility of the body is no longer necessary for the own-body-size effect. However, the question remains as to whether a visible body is necessary to *induce* a recalibration of visuospatial perception. In the presence of ownership, the visible body could have acted as a familiar size cue to initiate the rescaling of external space. On the other hand, in line with our hypothesis, a visible body might not be necessary for the initial visual recalibration of external space to occur. We hypothesized that similar to body-ownership, the effect of body size depends on a multisensory mechanism that updates the link between the somatosensory defined body-space and the visually defined external space. In Study II we tested this hypothesis directly by combining the invisible body illusion with the small-body illusion and the large-body illusion.

We found that despite the lack of a visible body, the own-body-size effect could still be induced. Participants experienced ownership of a small invisible body and a large invisible body after synchronous visuotactile stimulation, but not after asynchronous visuotactile stimulation. Object size estimations differed significantly between synchronous and asynchronous conditions. Target objects were perceived to be larger during the small invisible

body illusion, and to be smaller during the large invisible body illusion (Figure 10A). As in Study I, we found that the perceptual effect correlated positively with subjective measures of the ownership illusion (Figure 10B), which provides further evidence for the idea that the rescaling of visual space depends on body-ownership. Interestingly, the effect size in Study II was similar to the effect sizes found in Study I, which suggests that a visible body does not contribute at all to the induction of the own-body-size effect. Instead of a visible body being used as a familiar size cue to induce the own-body-size effect, the effect appears to be caused by visuotactile realignment and a direct coupling between body-space and external space. In the small invisible body, touches close to the camera are integrated with tactile sensations of the feet and legs. In order for such integration to occur, the representation of visual space needs to expand, causing all objects in space to be perceived as larger and further away. *Vice versa*, in the large invisible body illusion, touches far from the camera are integrated with these tactile sensations, which requires visual space to shrink. In summary, the results of Study II indicate that the own-body-size effect is induced through a recalibration of visual external space by realigning it to somatosensory body-space.

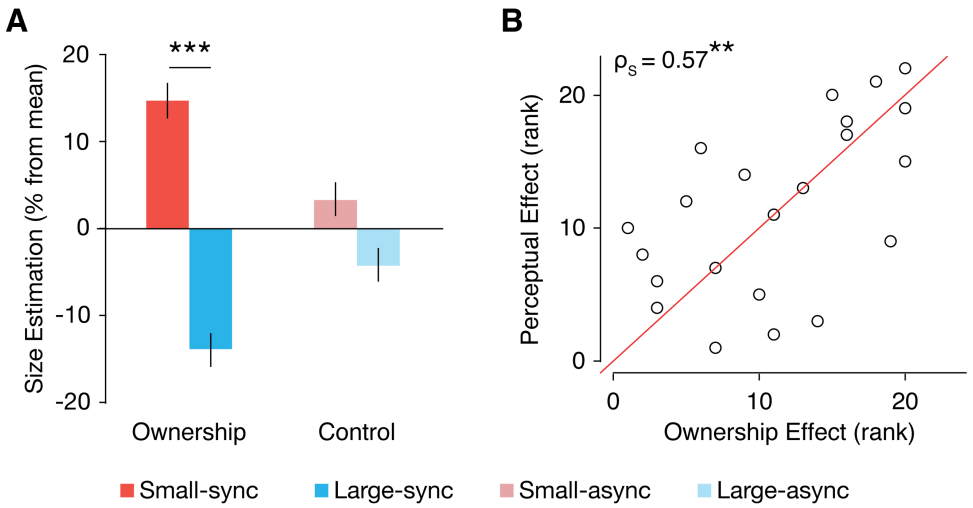

Figure 10. Main results of Study II. Bimanual size estimations as a percentage deviation from individual means (**A**), and the rank-based correlation between the ownership effect (illusion score difference between synchronous and asynchronous conditions) and the perceptual effect (interaction term between Small/Large and synchronous/asynchronous) (**B**). Small/Large = small and large artificial bodies; synchronous/asynchronous = synchronous and asynchornonous visuotactile stimulation. **p < 0.01, and ***p < 0.001.

4.3 STUDY III

Where the first two studies investigated the effect of body-ownership on visuospatial perception, the third study focused on its effect on visual awareness. Given that our own body is the most important visual object that exists – it is who we are – it seems a logical prediction that our brain prioritizes visual information from the body to reach awareness. To be more precise, we hypothesized that under identical visual stimulation, visual awareness should be promoted for a hand when ownership of that hand is experienced. We combined the rubber-hand illusion with binocular rivalry, in two separate experiments, to investigate this hypothesis.

In Experiment 1, we compared four conditions that differed solely on the presence or absence of the visual and tactile components of touch: visuotactile, visual-only, tactile-only, and no-stimulation. Ownership of the hand was successfully induced in the visuotactile condition, as measured by an ownership questionnaire. Crucially, the overall dominance of the hand percept was greatest in the visuotactile condition compared to all other conditions (Figure 11A). Further evidence for a direct effect of ownership on visual awareness was

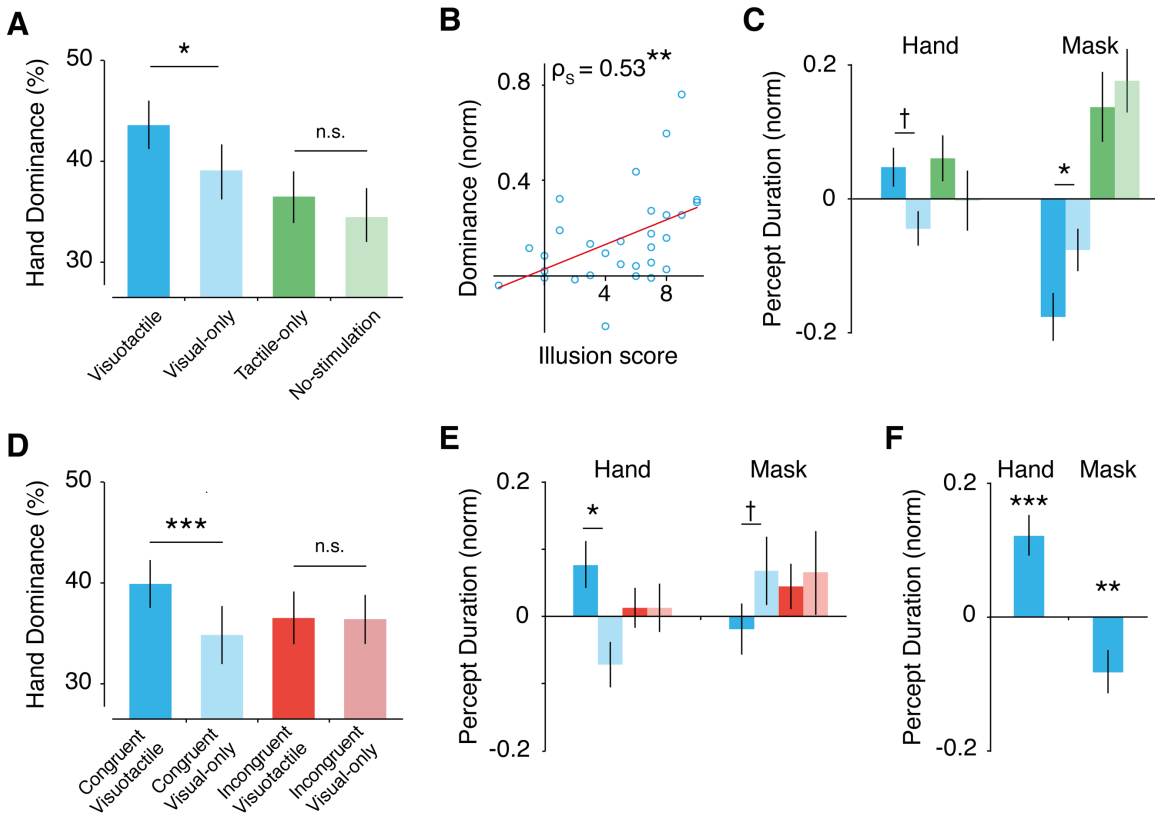

Figure 11. Main results of Study III. Overall dominance of the hand percept (**A**), the correlation between illusion score and overall dominance increase in the visuotactile condition compared to no-stimulation (**B**), and normalized percept durations in Experiment 1 (**C**). Overall dominance of the hand percept (**D**) and normalized percept durations (**E**) of Experiment 2. Combined percept durations of Experiment 1 and Experiment 2 for the (congruent) visuotactile condition normalized to the (congruent) visual-only condition (**F**). Colors refer to conditions specified in panels **A** and **D**. †p = 0.06, *p < 0.05, **p < 0.01, ***p < 0.001, and n.s. = not significant.

obtained from a positive correlation between subjective ownership ratings and the overall dominance increase in the visuotactile condition (Figure 11B). In Experiment 2, we compared the effect of synchronous visuotactile stimulation on a congruent hand image with its effect on an incongruent hand image (congruent visuotactile vs congruent visual-only, and incongruent visuotactile vs incongruent visual-only). Ownership ratings were higher for the congruent visuotactile condition compared to the incongruent visuotactile condition. And again, overall dominance was highest for the condition in which ownership was perceived: the congruent visuotactile condition (Figure 11D). These effects of ownership on the overall dominance of the hand percept were driven by a combination of longer dominance durations and shorter suppression durations (Figure 11C,E,F). The reduced suppression durations indicate that ownership effectively increased the stimulus strength of the hand image, and that the effect of ownership cannot be explained by increased endogenous attention towards the hand. Furthermore, although we found that the switch rate was higher for conditions in which the moving tactile probe was part of the visual stimulus, no such difference was found for conditions with identical visual stimuli, which indicates that participants attended to the rivaling stimuli to a similar degree in different conditions.

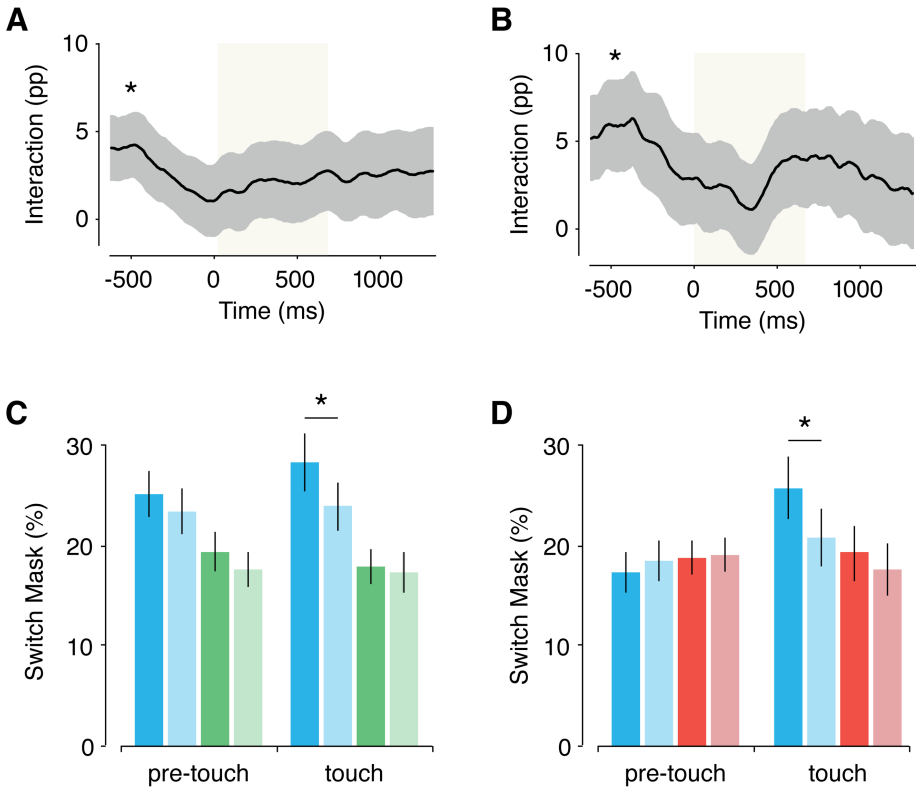

Figure 12 The effect of ownership (2x2 interaction term in Experiment 1 (**A**) and Experiment 2 (**B**)) before and after the onset of individual touches (t = 0-667 ms). The effect of individual touches on the probability of a perceptual switch from mask to hand, split for pre-touch period (-667 – 0 ms) and touch period (0 – 667 ms) in Experiment 1 (**C**) and Experiment 2 (**D**). Colors refer to conditions specified in Figure 9A,D (blue = visuotactile; light-blue = visual-only; green = tactile-only; light-green = no-stimulation; red = incongruent visuotactile; light-red = incongruent visual-only). * $p < 0.05$.

Further analyses separated the continuous effect of ownership from the transient effect of single touches. We utilized the exact knowledge of the onset and duration of individual touches to calculate the dominance of the hand percept before (-667 – 0 ms), during (0 – 667 ms), and after (667 – 1334 ms) a single touch. We observed that the visual component of single touches (i.e. motion of the tactile probe) caused a transient dominance increase of the hand percept. Importantly, we also found an independent continuous effect attributable to ownership itself, defined as the interaction-term in both experiments (Experiment 1: [visuotactile – visual-only] – [tactile-only – no-stimulation]; Experiment 2: [congruent visuotactile – congruent visual-only] – [incongruent visuotactile – incongruent visual-only]), which could not be explained by single touches (Figure 12A,B). In fact, this interaction effect was highest before the onset of a touch, which shows that the visual and tactile component of a single touch increased dominance only temporarily, whereas the effect of ownership was continuous. Next, we investigated the effect of single touches on individual percepts, by calculating the percept-stability when the hand was perceived, and the likelihood of a perceptual switch when the mask was perceived, both before (-667 – 0 ms) and during (0 – 667 ms) a touch. We found that single touches increased the stability of hand percepts, which was independent of the additional effect of ownership (i.e., no interaction-effect). Furthermore, single touches increased perceptual switches if a mask was perceived, but only when ownership was present (Figure 12C,D). Thus, individual touches increased dominance durations independent of ownership, and they reduced suppression durations only when ownership was present. This latter finding shows that, in the presence of ownership, multisensory integration occurs between a suppressed visual stimulus and conscious tactile stimulation.

In summary, ownership of the hand promotes visual awareness of that hand. It does so by lengthening individual percepts of the hand, and by shortening its suppression. This pattern of results suggests that ownership effectively increases the stimulus strength of the hand image. Furthermore, the results were specific to ownership of the hand, and could not be attributed to single visuotactile events, nor could they be explained as an attentional effect.

4.4 STUDY IV

In Study IV we aimed to induce ownership of a hand through visuotactile stimulation in the absence of visual awareness. The rationale for the possibility of such unconscious ownership was partly based on the results of Study III: visual information from a suppressed hand can be integrated with tactile information. And it was partly based on studies that describe the processing of visual information, and the occurrence of multisensory integration, outside the realms of visual awareness (see section 1.3.2). We combined the rubber hand illusion with continuous flash suppression (CFS), such that all visual information that is relevant for the illusion was suppressed, i.e. the hand and the tactile probe that touches it. Unconscious ownership was measured by proprioceptive drift and by SCR to a knife threat.

In Experiment 1a, we compared two conditions that differed solely on the orientation of the hand image: congruent and incongruent. In the congruent condition, after one minute of tactile stimulation, participants perceived the location of their veridical hand to be shifted towards the location of the hand image (i.e. proprioceptive drift), and they displayed autonomous fear responses to knife threats at the location of the suppressed hand (i.e. SCR) (Figure 13). Crucially, both proprioceptive drift and SCRs were significantly reduced in the incongruent condition. Thus, unconscious ownership could be induced for a masked congruent hand, but not for a masked incongruent hand.

In Experiment 1b, the mask was removed to render the hand clearly visible to participants. Again, participants showed proprioceptive drift and SCRs in the congruent condition but not in the incongruent condition. Interestingly, the effects in Experiment 1b were of similar magnitude as the effects in Experiment 1a, suggesting that visual awareness did not increase ownership in this study. Participants in Experiment 1b also subjectively reported stronger sensations of ownership during the congruent condition compared to the incongruent condition, as measured by an ownership questionnaire.

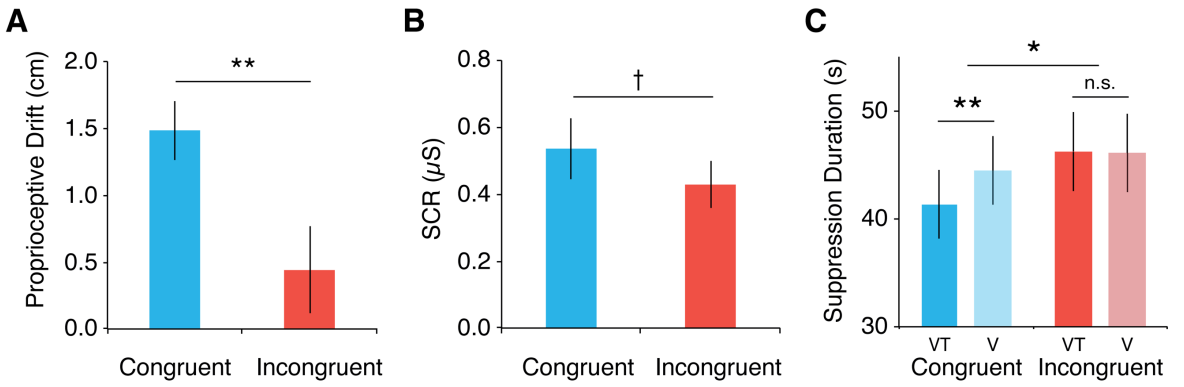

Figure 13. The main results of Study IV. Mean proprioceptive drift (**A**) and skin conductance response (**B**) in the congruent (blue) and incongruent (red) condition of Experiment 1a. Mean suppression duration during visuotactile conditions (dark shading) and visual-only conditions (light shading) in Experiment 2 (**C**). *p < 0.05, **p < 0.01, †p = 0.06.

Next, in Experiment 2, we assessed the effect of unconscious ownership on visual awareness by measuring the suppression duration of the hand during CFS. This suppression duration was measured on four conditions: congruent visuotactile, congruent visual-only, incongruent visuotactile, and incongruent visual-only. We found that, while suppressing all relevant visual information, synchronous visuotactile stimulation reduced suppression durations but only when the suppressed hand had a congruent orientation. Thus, the condition in which unconscious ownership could be measured in Experiment 1a, also hastened the rescue from suppression of the hand-image in Experiment 2. This suggests that, similar to conscious ownership (Study III), unconscious ownership can boost the hand into visual awareness.

5 DISCUSSION

Body-ownership and visual perception have been major topics in philosophy and psychology for centuries. Although their possible interaction was first formalized "only" 300 years ago, the assumption that our body size somehow defines our visual perception, e.g. the intuitive idea that a child perceives the world differently than an adult, must be as old as mankind. However, it was not until the recent development of body-ownership illusions, that these intuitions and assumptions could be subjected to scientific endeavors. By effectuating these illusions, the four studies that comprise this thesis contribute to our understanding of the role of body-ownership in visual perception, and the role of visual perception in body-ownership. In Study I and II we investigated the mechanisms by which body-ownership causes the perceived size of the world to scale inversely to the size of our body. In Study III we showed that body-ownership can boost visual awareness. And in Study IV we found evidence for unconscious body-ownership, i.e. body-ownership in the absence of visual awareness.

5.1 BODY-OWNERSHIP AND VISUOSPATIAL PERCEPTION

The own-body-size effect states that the perceived size of the world is inverse to the size of our own body, such that the world looks larger to a small observer, and *vice versa*, the world looks smaller to a large observer. By inducing full-body illusions with different sized artificial bodies, it was shown that body-ownership is necessary to maximize this effect of body-size (van der Hoort et al., 2011). In Study I and II we investigated the relative contribution of four possible mechanisms by which body-ownership could potentially contribute to changes in visuospatial perception. First, the body, as seen from the natural first person perspective, could serve as a stronger familiar size cue when ownership of that body is experienced (Study I, Experiment 1). Second, oculomotor cues could play a stronger role in the presence of body-ownership (Study I, Experiment 2). Third, the observed body might function as a strong familiar size cue in order to *initiate* a perceptual rescaling of external space (Study II). These three mechanisms could not explain our findings. Instead, the results of Study I and Study II are only congruent with a fourth mechanism: The spatial realignment of vision and touch, which is necessary for the induction of body-ownership illusions, automatically updates visual space beyond the body by a direct link between body-space and external space. Importantly, this recalibration of external space is independent of the distance from the observer (Study I, Experiment 3). The clearest demonstration of this mechanism was shown in Study II. In the invisible small body illusion, the observed touch is initially nearer than the felt touch, and therefore external space must be expanded in order to perceive a single visuotactile that is applied to one's own body. *Vice versa*, in the large invisible body illusion, the observed touch is initially observed further away than the felt touch, and the representation of external space needs to be shrunken. The representation of object size and distance is thought to be automatically updated with the updated representation of visual space, such that they expand in the small-body illusion and shrink in the large-body illusion. In this sense, the own-body

size effect exemplifies that touch and proprioception can dominate vision, which is opposite to the dominant role of vision in most ownership illusions (see section 1.1.3). To illustrate the reciprocity between external space and body size, the own-body-size effect can also be viewed from an external (allocentric) perspective. The own body can be viewed as providing 'a system of axes of coordinates' in which external space is represented. Having a smaller body, effectively shrinks the three-dimensional grid that such axes of coordinates define. As a result, the same object now fills more grid-cells that comprise external space, and will therefore be perceived as larger. This idea is visualized in Figure 14.

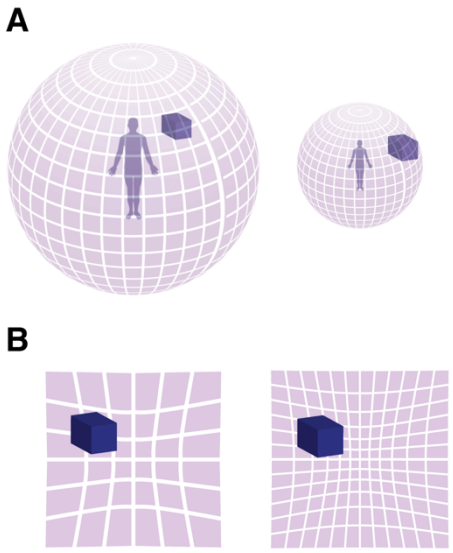

Figure 14 The own-body-size effect seen from an allocentric perspective (**A**) and from an egocentric perspective (**B**).

Despite the consistent use of visuotactile ownership illusions in Study I and II, the inter-sensory recalibration that underlies the own-body-size effect does not necessarily depend on visuotactile realignment. In ownership illusions that use visuomotor synchrony (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012; Tsakiris, Prabhu, & Haggard, 2006), a visuomotor realignment might similarly recalibrate the visual perception of space. For example, in virtual reality studies, the embodiment of a small virtual hand or a child-like avatar changes visual perception in a similar manner as the small-body illusion (Banakou et al., 2013; Linkenauger et al., 2013). Following the logic of sensory realignment described above, in these studies the attribution of an initiated movement ("I'm moving my hand") to an observed movement close by ("I see a hand moving, it must be mine"), expands the representation of visual space in a similar manner as in the small-body illusion.

How does this sensory realignment mechanism fit with existing theories on the nature of visuospatial perception as described in the introduction? Sensorimotor contingency theories emphasize the learned association between action and perception (e.g. Held, 1961; Noë, 2010). According to these theories, the nature of visual perception is to know how visual input

will change with movement, and this knowledge is acquired through lifelong experience. Our findings show that the own-body-size effect does not necessarily depend on movement of the body, i.e. visuomotor realignment is merely one possible way to rescale visuospatial perception, as mentioned above. Furthermore, the own-body-size effect does not require extensive learning of sensorimotor contingencies. Since, in the typical experiment, participants switch between bodies every few minutes, extensive exposure does not appear necessary. Thus, the own-body-size effect cannot be explained by sensorimotor contingency theories, however, this does not mean that sensory contingencies do not contribute to visuospatial perception at all. The perceived size of objects during the small-body illusion was between 126% and 220% of their perceived size during the large-body illusion, whereas theoretically 500% would be expected since the large artificial body is five times larger than the small artificial body. In other words, the effect of visuotactile realignment does not entirely override the learned associations between retinal information (i.e. retinal size and distance cues) and size perception, which themselves might depend on sensorimotor contingencies.

Efferent readiness theories fit better with the own-body-size effect. Swapping to a smaller body, as in the small-body illusion, changes the action possibilities of the observer. According to efferent readiness theories, the perceived size of an object increases because the necessary movements to interact with that object change (Gibson, 1979; Grush, 2000; Proffitt, 2006; Taylor, 1962). A 400-cm giant might need one hand, or only two fingers, to grasp an object whereas an 80-cm dwarf would need two hands. Similarly, the giant would need four steps to cover a certain distance, whereas the dwarf needs twenty. Importantly, most efferent readiness theories do not require these action possibilities to be learned through experience, as is the case for the ecological vision theory (Gibson, 1977, 1979). A giant perceives an object as smaller because it affords a different action, without the need of having ever performed that specific action to that specific object. In contrast, the energy-cost based perception theory (Proffitt, 2006) seems more likely to require some experience with action, in order to know its consequences on energy usage. Thus, although we all experienced a small body as a child, explaining the perceptual changes in the large body illusion seems more difficult for this theory. The theory that suits our interpretation of the own-body-size effect best is the disposition theory (or skill theory, (Grush, 2000, 2007)). According to this theory, the representation of space is not purely sensory, nor is it purely motoric. It is a higher order *manifold* in which different senses as well as (possible) actions are represented. The nature of spatial perception lies in the relation between different senses and motor programs. Interestingly, the disposition theory claims that such a representation of space automatically causes an observer to have knowledge of being a subjective entity in an objective world, and of what constitutes the subjective self and what constitutes objective space (Grush, 2000). This idea is closely related to a more functional definition of body-ownership, i.e. to know what constitutes oneself and what constitutes the external world, which will be discussed in more detail below when interpreting the findings of Study IV.

What could be the neural mechanisms of the own-body-size effect? Body-ownership relies on multisensory integration of visual, tactile, and proprioceptive signals. This multisensory

integration takes place in multisensory brain areas in the premotor cortex (PMC) and the intraparietal sulcus (IPS), resulting in a coherent body representation (Ehrsson et al., 2004; Lloyd, Shore, Spence, & Calvert, 2002; Petkova, Björnsdotter, et al., 2011). Crucially, the subjective experience of ownership correlates with activity in these areas during ownership-illusions (Petkova, Björnsdotter, et al., 2011). During the small-body illusion and the large-body illusion, these body representations are updated. Two possible feedback loops might convey information about the updated body-representation to affect visuospatial perception. First, this information could be fed back to the medial and lateral temporal cortex and the medial parietal cortex, which represent external space in egocentric and allocentric coordinates (Burgess, Maguire, & O'Keefe, 2002; Galati, Pelle, Berthoz, & Committeri, 2010; Kravitz, Saleem, Baker, & Mishkin, 2011; Maguire et al., 1998; Moser, Kropff, & Moser, 2008). Subsequently, the updated representation of external space would be fed back to visual areas in the parietal and occipital cortex that process object size information (Julian, Ryan, & Epstein, 2016; Konen & Kastner, 2008; Murray, Boyaci, & Kersten, 2006). In parallel, the updated body-representation could directly inform visual areas that process object size information. Although this latter possibility would not explain why the entire spatial layout is rescaled in the own-body-size effect, it could explain the changed size perception of objects when viewed in relative isolation of surrounding visuospatial cues.

Informing these visual areas about the new body size might result in altered response properties of individual neurons. Groups of neurons in the visual cortex that comprise a voxel in functional magnetic resonance imaging (fMRI) are responsive to specific locations of the retina, i.e. they have a population receptive field (pRF). It has been shown that such pRFs are not fixed, but can be modulated by object size illusions (Murray et al., 2006) and attention (de Haas, Schwarzkopf, Anderson, & Rees, 2014). In an unpublished fMRI study, we used retinotopic mapping to measure both the size and the eccentricity (i.e. the radial distance from fixation) of pRFs for voxels in the visual cortex (V1, V2, V3a, V3b, and V4) during the small-body illusion and the large-body illusion. The rationale was that an increased pRF size during the small-body illusion would recruit more neurons to represent the same object, and therefore make the object appear larger. Similarly, a decrease in pRF eccentricity of single voxels in the small-body illusion would also lead to an object being represented by more neurons. Following this logic, the opposite pattern was hypothesized for the large-body illusion. Albeit a very intriguing hypothesis, our findings were inconclusive for either effect. One methodological limitation that might have contributed to this null-finding is the relatively narrow field of view of MR-compatible HMDs. This is a problem because they offer little space for the visual presentation of an artificial body located in a room in which there is a screen that displays the retinotopic mapping stimuli. As a result, and perhaps magnified by the need to scan the whole brain in order to confirm activity in multisensory brain regions associated with ownership, pRF estimations were only reliable in V1, V2, and V3b. It is very possible that perceptual changes are not reflected by activity in these early visual areas but instead depend on activity in higher visual areas.

The own-body-size effect shows some striking similarities with the Alice in Wonderland syndrome (AIWS) (Todd, 1955). And hence, the brain areas associated with this perceptual disorder might be suggestive of the underlying brain mechanisms of the own-body-size effect. AIWS is characterized by misperceptions of body-space and visual space, although specific symptoms vary between patients. Similar to Alice in the famous eponymous novel, typical AIWS patients perceive their body (or body-parts) to be much larger or smaller than usual (macrosomatognosia and microsomatognosia). In addition, objects may appear much smaller or larger than they actually are (micropsia and macropsia), or they may appear much nearer or further (telopsia and pelopsia). Macrosomatognosia and microsomatognosia can be interpreted as misrepresentations of body-space, whereas micropsia, macropsia, telopsia, and pelopsia can be viewed as misrepresentations of visual-space. These symptoms can co-occur in a pattern that follows the logic of the own-body-size effect, but may also appear in isolation. The most common causes of AIWS are migraine, Epstein-Barr virus infections, and strokes (Mastria, Mancini, Viganò, & Di Piero, 2016). Interestingly, AIWS is associated with disturbances in parietal areas, including the IPS, which relate to the distortions of body-space, and disturbances in occipital areas that relate to the visual distortions of object size and distance. For this reason, it has been proposed that AIWS reflects the impaired integration of visual and somatosensory information (Mastria et al., 2016), which could be based on specific disturbances around the parietal-occipital junction where body-space seems to interact with visual space (Chen, Weidner, Weiss, Marshall, & Fink, 2012).

The own-body-size effect might also play an important role in the retrieval of autobiographical memory. In the introduction, I described a phenomenon that most people have experienced themselves: the surprise at how small the house that you grew up in appears when you revisit it as an adult. Given that our body scales the perceived size of our environment, this is not hard to explain. During the encoding of that childhood memory your body was small, and therefore your room appeared spacious, but now, standing in your old room again, it does not appear that big anymore. You *remembered* your room to be larger. Just as the spatial content of our current visual perception, the spatial content of our autobiographical memories is represented relative to our body-size. In other words, autobiographical memories seem to be encoded in a certain *body-context*, i.e. the spatial relation between the size of your body and the physical size of the world around you. As your body grows, this body-context changes accordingly. Therefore, similar to other well-known context-dependency effects on memory (Godden & Baddeley, 1975; Nyberg, Habib, McIntosh, & Tulving, 2000; Tulving & Thomson, 1973; Wheeler, Petersen, & Buckner, 2000), the congruence between the body-context during encoding and retrieval might facilitate memory retrieval. This could explain *childhood amnesia*, i.e. the difficulty of remembering childhood memories as an adult (Howe & Courage, 1993; Morrison & Conway, 2010; Rubin, 1982), since our current body-context is incongruent with that of our childhood. In an ongoing study, we are testing this specific hypothesis by using the small-body illusion (van der Hoort et al., 2011; and Study I) to facilitate the retrieval of childhood memories. Comparing the small-body illusion with the traditional full-body illusion (Petkova & Ehrsson, 2008), the initial results indeed reveal such a body-context effect on

autobiographical memory retrieval. To be specific, in the small-body-illusion, participants retrieve childhood memories from a younger age, and memories from the same age are recalled more vividly, i.e. they have a greater episodic quality (Bergouignan, van der Hoort, & Ehrsson, 2013). Importantly, these effects disappear when ownership of the small body is disrupted by asynchronous visuotactile stimulation. Given these initial results, the small-body illusion might be applicable in clinical psychology, especially for mood and anxiety disorders that have been caused by childhood trauma (Heim & Nemeroff, 2001).

5.2 BODY-OWNERSHIP AND VISUAL AWARENESS

In Study III we combined the classical rubber hand illusion with binocular rivalry to show that ownership of a hand promotes visual awareness of that hand. The conclusion that the increase in overall dominance of the hand image was truly the consequence of ownership is based on several converging results.

First, the overall dominance increase in the presence of ownership was driven both by increased dominance durations as well as by decreased suppression durations. Decreased suppression durations are specifically associated with increased stimulus strength, similar to the effect of increased contrast (Levelt, 1965), spatial frequency (Fahle, 1982), and luminance (O'Shea et al., 1994). Importantly, suppression durations cannot be explained by voluntary top down attention (Ooi & He, 1999). Another reason why top down attention could not have mediated the effect of ownership is that this would result in a higher switch rate (Ooi & He, 1999), however, we found similar perceptual switch rates for conditions with identical visual stimuli but different levels of ownership.

The second finding that is in line with our conclusion is the correlation between overall dominance increase and strength of the ownership illusion. Participants that reported the strongest sensation of ownership also had the greatest dominance increase of the hand image. It seems unlikely that participants felt more ownership *because* they saw the hand more often, for two reasons. First, the correlations were performed on the increased overall dominance, not on the absolute time they saw the hand. And second, the subjective report was carried out after a 120-s trial, which, even if participants saw the hand merely 25% of the time, should be enough to induce ownership. Importantly, participants reported their subjective experience of ownership only after all binocular rivalry data was collected, i.e. participants were naïve to the concept of body-ownership illusions during the main experiment, and the rivalry data can therefore not have been influenced by a response bias.

The third source of evidence comes from our analysis of the effect of single touches (visuotactile events) on the overall dominance of the hand image. Although single visuotactile events increased the overall dominance of the hand, the effect of ownership (statistically defined as the interaction term in the 2x2 factorial designs of both experiments) was greatest before the onset of such an event. This suggests that the effect of single touches, and that of their unisensory components, was fixed to the touch-onset and transient in nature. In

contrast, ownership itself had a continuous effect, independent of single touches, that was relatively larger before the onset of touch.

Finally, the very effect of single visuotactile events on suppression was modulated by ownership. Only when ownership was present did a single touch rescue the hand from suppression. This is indicative of two fascinating phenomena. It shows that multisensory integration has occurred between the suppressed visual stimulus and the consciously perceived tactile event. And it also shows that ownership of the hand is maintained during suppression. This finding encouraged us to pursue the unconscious hand-ownership illusion, as discussed below. In contrast to suppression durations, the effect of visuotactile events on dominance durations was independent of ownership. This does not mean that ownership had no effect on dominance durations – it did – but instead, that ownership and single visuotactile events contributed independently.

Taken together, these four results converge to the conclusion that ownership itself promotes visual awareness. The temporal characteristics of our findings are in line with the idea that ownership effectively increases the stimulus strength of the hand image. Alternatively, one might argue that instead of reflecting an increased stimulus strength, the effect of body-ownership should be interpreted as a contextual effect. The visual context of two rivaling stimuli increases the overall dominance of the stimulus that is congruent with that context (Sobel & Blake, 2002). In Study III, the effect in the visual-only condition is an example of such an effect. The tactile probe, which was continuously visible because it was present in both eyes, served as a visual context that boosts the dominance of the hand image in the visual-only condition. This shows that the tactile probe contextualized better with the hand image than with the mask, especially when the tactile probe was moving. Similarly, one might argue, tactile sensations provide a more potent (cross-modal) context for the hand in case ownership of that hand is experienced. However, congruent contexts lengthen dominance durations but leave suppression durations relatively unaffected (Sobel & Blake, 2002). Thus, based on the decreased suppression durations found in Study III, the effect of ownership is best explained as resulting in an increased stimulus strength of the hand image, rather than providing a better multisensory context for that hand image.

The effect of ownership on visual awareness should be differentiated from simple cross-modal interactions on binocular rivalry as described in the introduction. When the sound of a birdsong increases the visibility of a bird image (Chen et al., 2011), it seems unlikely that one singing bird is perceived. Similarly, when the smell of a rose increases the visibility of a rose image (Zhou et al., 2010), do participants really perceive the odor to originate from the image? Such effects could be explained by simple facilitating associations between different senses. This would be analogue to an effect in the tactile-only condition of Experiment 1 in Study III, i.e. if simply being touched on the hand would increase visual awareness of hand images in general (we did not find such an effect). In contrast, the effect of ownership could be described as an example of multisensory awareness (Deroy et al., 2016), in which the multisensory integration of vision, touch, and proprioception leads to the unitary percept of

"my hand", which subsequently increases the signal intensity of visual information from that hand. However, as Experiment 2 in Study IV shows, ownership of a hand does not necessarily need to be consciously perceived for it to promote visual awareness of that hand. Thus, instead of claiming the necessity for multisensory awareness for the effect of body-ownership shown in Study III, the minimal requirement seems to be the unitary representation of the body, based on multisensory integration, be it accompanied by a conscious experience of it or not.

The claim that body-ownership can occur outside the realm of awareness is based on the results of Experiment 1a in Study IV. In this experiment, the proprioceptively perceived location of participants' veridical hand shifted towards the location of the suppressed hand image. In addition, participants displayed an autonomous fear response to a knife threat in the location of the suppressed hand. These implicit measures are standard ways to quantify body-ownership (e.g. Botvinick & Cohen, 1998; Petkova & Ehrsson, 2008; van der Hoort et al., 2011). However, the standard definition of body-ownership refers to it as the subjective experience of owning a body (Gallagher, 2000). Thus, to state that body-ownership can occur outside of awareness requires an alternative, more functional definition: Ownership is the ability of an organism to dissociate between body-space and external space, i.e. to have knowledge of the boundaries of the body in spatial coordinates, which in itself does not depend on a conscious experience. Such 'functional ownership' does not necessarily require different underlying mechanisms. As described in the introduction, the representation of the body is thought to arise from multisensory integration of vision, touch, and proprioception (Ehrsson, 2012). And although multisensory integration is typically investigated during perceptual awareness of those senses, awareness itself might not be necessary. In fact, there is no reason why ownership could not be induced when both visual stimulation and tactile stimulation are masked (D'Amour & Harris, 2014), since multisensory integration can occur in complete unawareness (Faivre et al., 2014).

The unconscious ownership illusion is in line with the anatomical rule and the perspective rule of ownership, which reflect the integration of the masked hand with proprioceptive information. However, the results of Study IV cannot conclude that unconscious ownership, albeit induced by synchronous visuotactile stimulation, follows the spatial rule and the temporal rule to a similar degree as the conscious rubber hand illusion. For example, is the temporal resolution of unconscious visual processes high enough to dissociate between synchronous and asynchronous visuotactile stimulation? Similarly, is it necessary for the masked visual touch and the felt touch to occur on corresponding fingers, i.e. does unconscious ownership follow the spatial rule of multisensory integration? Future studies should aim to answer these open questions.

Another consideration of the unconscious ownership illusion concerns the assessment of visual awareness. Participants were instructed to report the orientation of the hand as soon as they could, and analyses were only performed on trials in which participants did not respond. Could participants have seen small parts of the masked stimulus, without being able to detect

the orientation of the hand? If participants had seen the moving object, they must have seen patches of skin as well, because the moving object was black and therefore only visible by contrast of the hand (which itself was on a black background). Furthermore, if participants were aware of small patches of skin, following the moving object, they would effectively have seen the hand in a searchlight manner. Touches were applied from the back of the hand to the tip of the index-finger. Given that the moving object was wider than a finger but not wider than the back of the hand, the index-finger should be dissociable from the back of the hand in such searchlight-like visual awareness, and therefore hand orientation should be detectable. Thus, the specific design of the visual stimuli makes it unlikely that orientation of the hand would not be detected if local breaks through suppression had occurred. In addition, such local breaks through suppression would not explain why the orientation of the masked hand influenced proprioceptive drift and SCRs. And finally, local breaks through suppression, in the absence of hand orientation detection, would not explain why a congruent hand breaks through suppression faster (Experiment 2). Taken together, it seems unlikely that local breaks through suppression that may have occurred in Study IV could explain our results. Nevertheless, in follow-up investigations of the temporal rule and spatial rule of unconscious ownership, it would be a good idea to assess these local breaks through suppression more directly, perhaps by having participants report movement instead of hand orientation.

Taken together, the results of Study III and Study IV reveal an intriguing interplay between ownership and visual awareness. On the one hand, ownership promotes visual awareness, but on the other hand, visual awareness is not necessary for ownership. What could be the neural mechanisms of these findings? Let us first consider the effect of hand-ownership on visual awareness of that hand. Conscious hand-ownership results from multisensory integration in IPS and PMC (Ehrsson, 2012; Ehrsson et al., 2004; Gentile et al., 2013; Petkova, Björnsdotter, et al., 2011), whereas the visual perception of hands is associated with activity in the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001), which is a functionally defined area in the lateral occipital complex (LOC). The EBA is also able to dissociate between one's own hand and someone else's hand (Downing et al., 2001; Myers & Sowden, 2008). Interestingly, during the rubber hand illusion, functional connectivity between the IPS and the EBA is increased, indicative of increased communication between those areas (Gentile et al., 2013; Guterstam et al., 2013). Therefore, it is plausible that feedback from the IPS increases the signal-to-noise ratio of the hand image. Since suppressed objects are still processed by the LOC (Fang & He, 2005), this would lead to both increased dominance duration and decreased suppression durations. The idea that ownership promotes visual awareness through increased feedback from the IPS to the EBA fits with the *recurrent processing theory* of consciousness (Lamme, 2006; Lamme & Roelfsema, 2000). According to this theory, the initial feedforward current of visual information from early visual areas to higher visual areas, and from the visual cortex to nonvisual brain areas, is not sufficient to induce visual awareness. Only when information is fed back to (early) visual areas through recurrent processing does awareness of the visual stimulus arise (Lamme, 2006; Lamme & Roelfsema, 2000; van Loon, Scholte, van Gaal, van der Hoort, & Lamme, 2012).

In line with this theory of visual awareness, recurrent processing from the IPS to the EBA would cause awareness of the hand-image.

How then is ownership induced in the absence of visual awareness? Somehow, the suppressed visual stimulus needs to arrive in the IPS in order to be integrated with tactile and proprioceptive information. The minimal visual information that is required to survive during suppression is the shape and orientation of the hand, and the movement of the tactile probe. The shape and orientation of the suppressed hand is processed by the brain (Salomon et al., 2013), probably in the EBA, since objects are still processed in the LOC during suppression (Fang & He, 2005). Subsequently, this information could travel towards the IPS along the dorsal stream, as has been shown for tools (Fang & He, 2005). Motion information is also processed during suppression (Itoh et al., 2005; Kaunitz et al., 2011; Koivisto et al., 2010; Maruya et al., 2008), and this information might reach motion-sensitive areas in the IPS (Shulman et al., 1999). Thus, the required visual information would reach the IPS and be integrated with tactile and proprioceptive information to induce unconscious ownership. The effect of such unconscious hand-ownership on visual awareness of the hand, as shown in Experiment 2 of Study IV, are thought to use identical mechanisms as described for the effect of conscious ownership.

Despite the fact that both conscious ownership and unconscious ownership might rely on multisensory integration in the IPS, they are phenomenologically very different. This phenomenological difference might be due to a combination of two factors. First, conscious ownership might simply be due to stronger activity in the IPS. And second, additional brain areas could be needed for ownership to reach awareness. For example, areas in the premotor cortex that have been associated with body-ownership (Ehrsson et al., 2005, 2004) might be necessary to become fully aware of it, and perhaps in combination with prefrontal areas, could enable the participant to report on those experiences (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006).

5.3 CONCLUSIONS

The main aim of this thesis was to assess the effect of body-ownership on visual perception. Body-ownership plays an important role in visuospatial perception, by inversely scaling the perceived size of the world to the size of the own body. This recalibration reflects a link between body-space and visual space that depends on the alignment of somatosensory information and visual information. Body-ownership was also shown to promote visual awareness, by increasing the stimulus-strength of visual information from the body. In addition to these effects of ownership on visual perception, we established a novel paradigm in which ownership is induced for a hand that is not consciously perceived because it is suppressed by a mask. This unconscious rubber hand illusion relies on visuo-tactile-proprioceptive integration in the absence of visual awareness. These findings contribute to the understanding of the nature and mechanisms of both visual perception and body-ownership.

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7 REFERENCES

Alsius, A., & Munhall, K. G. (2013). Detection of audiovisual speech correspondences without visual awareness. *Psychological Science*, *24*(4), 423–431.

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proceedings. Biological Sciences*, *270*(1523), 1499–1506.

Arnold, D. H., Grove, P. M., & Wallis, T. S. A. (2007). Staying focused: a functional account of perceptual suppression during binocular rivalry. *Journal of Vision*, *7*(7), 7.1-8.

Arzy, S., Overney, L. S., Landis, T., & Blanke, O. (2006). Neural Mechanisms of Embodiment. *Archives of Neurology*, *63*(7), 1022.

Bach-y-Rita, P. (2004). Tactile sensory substitution studies. *Annals of the New York Academy of Sciences*, *1013*(1), 83–91.

Bach-y-Rita, P., & W. Kercel, S. (2003). Sensory substitution and the human-machine interface. *Trends in Cognitive Sciences*, *7*(12), 541-546.

Bajcsy, R., & Lieberman, L. (1976). Texture gradient as a depth cue. *Computer Graphics and Image Processing*, *5*(1), 52–67.

Banakou, D., Groten, R., & Slater, M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(31), 12846–12851.

Bergouignan, L., van der Hoort, B., & Ehrsson, H. H. (2013). Boosting recall of childhood memories with a child-size body illusion. In *Society for Neurosciece*. San Diego.

Berkeley, G. (1709). An Essay Towards a New Theory of Vision. In D. Clarke (Ed.), *Berkeley: Philosophical Writings*. Cambridge: Cambridge University Press.

Bhalla, M., & Proffitt, D. R. (1999). Visual-motor recalibration in geographical slant perception. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1076–1096.

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, *3*(1), 13–21.

Blake, R., Westendorf, D. H., & Overton, R. (1980). What is Suppressed during Binocular Rivalry? *Perception*, *9*(2), 223–231.

Blake, R., Zimba, L., & Williams, D. (1985). Visual motion, binocular correspondence and binocular rivalry. *Biological Cybernetics*, *52*(6), 391–397.

Bossink, C. J. H., Stalmeier, P. F. M., & de Weert, C. M. M. (1993). A test of Levelt's second proposition for binocular rivalry. *Vision Research*, *33*(10), 1413–1419.

Bottini, G., Bisiach, E., Sterzi, R., & Vallar, G. (2002). Feeling touches in someone else's hand. *Neuroreport*, *13*(2), 249–252.

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see. *Nature*, *391*(6669), 756–756.

Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The "laws" of binocular rivalry: 50 years of Levelt's propositions. *Vision Research*, *109*, 20–37.

Brenner, E., & van Damme, W. J. (1998). Judging distance from ocular convergence. *Vision Research*, *38*(4), 493–498.

Bridgeman, B. (2010). How the brain makes the world appear stable. *I-Perception*, *1*(2), 69–72.

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*(6), 719–722.

Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Research*, *31*(11), 1903–1913.

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*(4), 625–641.

Chen, Q., Weidner, R., Weiss, P. H., Marshall, J. C., & Fink, G. R. (2012). Neural interaction between spatial domain and spatial reference frame in parietal-occipital junction. *Journal of Cognitive Neuroscience*, *24*(11), 2223–2236.

Chen, Y. C., Yeh, S. L., & Spence, C. (2011). Crossmodal constraints on human perceptual awareness: Auditory semantic modulation of binocular rivalry. *Frontiers in Psychology*, *2*(SEP), 212.

Conrad, V., Bartels, A., Kleiner, M., & Noppeney, U. (2010). Audiovisual interactions in binocular rivalry. *Journal of Vision*, *10*(10), 27–27.

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*(2), 229–240.

Crick, F., & Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex (New York, N.Y.: 1991)*, *8*(2), 97–107.

Cutting, J. E., & Vishton, P. M. (1995). Perceiving layout and knowing distances: The integration, relative potency, and contextual use of different information about depth. In W. Epstein & S. Rogers (Eds.), *Perception of space and motion.* (pp. 69–117). San Diego: Academic Press.

D'Amour, S., & Harris, L. R. (2014). Vibrotactile masking through the body. *Experimental Brain Research*, *232*(9), 2859–2863.

de Haas, B., Schwarzkopf, D. S., Anderson, E. J., & Rees, G. (2014). Perceptual load affects spatial tuning of neuronal populations in human early visual cortex. *Current Biology*, *24*(2), R66–R67.

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–211.

Deroy, O., Faivre, N., Lunghi, C., Spence, C., Aller, M., & Noppeney, U. (2016). The Complex Interplay Between Multisensory Integration and Perceptual Awareness. *Multisensory Research*, *29*(March), 1–22.

Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *Progress in Brain Research*, *140*, 165–180.

Dieter, K. C., & Tadin, D. (2011) Understading attentional modulation of binocular rivalry: a framework based on biased competition. *Frontiers in Human Neuroscience, 5*, 155.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A Cortical Area Selective for Visual Processing of the Human Body. *Science*, *293*(5539), 2470–2473.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A Cortical Area Selective for Visual Processing of the Human Body. *Science*, *293*(5539).

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science (New York, N.Y.)*, *255*(5040), 90–92.

Dummer, T., Picot-Annand, A., Neal, T., & Moore, C. (2009). Movement and the Rubber Hand Illusion. *Perception* , *38*(2), 271–280.

Dunn, B. E., Gray, G. C., & Thompson, D. (1965). Relative height on the picture-plane and depth perception. *Perceptual and Motor Skills*, *21*(1), 227–236.

Dunphy, N., Evans, L., Klostermann, S., & Durgin, F. H. (2005). Visuo-spatial alignment produces an instant rubber hand illusion. *Journal of Vision*, *5*(8), 749–749.

Durgin, F. H., Evans, L., Dunphy, N., Klostermann, S., & Simmons, K. (2007). Rubber Hands Feel the Touch of Light. *Psychological Science*, *18*(2), 152–157.

Ehrsson, H. H. (2009). How Many Arms Make a Pair? Perceptual Illusion of Having an Additional Limb. *Perception*, *38*(2), 310–312.

Ehrsson, H. H. (2012). The Concept of Body Ownership and Its Relation to Multisensory Integration. In B. E. Stein (Ed.), *The New Handbook of Multisensory Processes* (pp. 775–792). Cambridge: MIT Press.

Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *25*(45), 10564–10573.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb. *Science*, *305*(5685), 875–877.

Fahle, M. (1982). Binocular rivalry: Suppression depends on orientation and spatial frequency. *Vision Research*, *22*(7), 787–800.

Faivre, N., Mudrik, L., Schwartz, N., & Koch, C. (2014). Multisensory integration in complete unawareness: evidence from audiovisual congruency priming. *Psychological Science*, *25*(11), 2006–2016.

Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, *8*(10), 1380–1385.

Farmer, H., Tajadura-Jiménez, A., & Tsakiris, M. (2012). Beyond the colour of my skin: How skin colour affects the sense of body-ownership. *Consciousness and Cognition*, *21*(3), 1242–1256.

Fisher, S. K., & Ciuffreda, K. J. (1988). Accommodation and Apparent Distance. *Perception*, *17*(5), 609–621.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology*, *76*(1), 141–57.

Frith, C. D., Blakemore, S. J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *355*(1404), 1771–1788.

Galati, G., Pelle, G., Berthoz, A., & Committeri, G. (2010). Multiple reference frames used by the human brain for spatial perception and memory. *Experimental Brain Research*, *206*(2), 109–120.

Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences*, *4*(1), 14–21.

Gayet, S., Van der Stigchel, S., & Paffen, C. L. E. (2014). Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. *Frontiers in Psychology*, *5*, 460.

Gentile, G., Guterstam, A., Brozzoli, C., & Ehrsson, H. H. (2013). Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *33*(33), 13350–11366.

Gibson, J. J. (1977). The theory of affordances. In R. Shaw & J. Bransford (Eds.), *Perceiving, Acting, and Knowning. Towards an Ecological Psychology.* Hillsdale: Erlbaum.

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.

Godden, D. R., & Baddeley, A. D. (1975). Context-dependent memory in two natural environments : on land and underwater. *British Journal of Psychology*, *66*(3), 325–331.

Goldstein, E., & Bruce, V. (1999). Perceiving visual space. In E. Goldstein & V. Bruce (Eds.), *Sensation and Perception* (pp. 215–231). Pacific Grove: Brooks/Cole Publishing Company.

Grush, R. (2000). Self, World and Space: The Meaning and Mechanismsof Ego- and Allocentric Spatial Representation. *Brain and Mind*, *1*(1), 59–92.

Grush, R. (2007). Skill theory v2.0: dispositions, emulation, and spatial perception. *Synthese*, *159*(3), 389–416.

Guterstam, A., Abdulkarim, Z., & Ehrsson, H. H. (2015). Illusory ownership of an invisible body reduces autonomic and subjective social anxiety responses. *Scientific Reports*, *5*(1), 9831.

Guterstam, A., Gentile, G., & Ehrsson, H. H. (2013). The Invisible Hand Illusion: Multisensory Integration Leads to the Embodiment of a Discrete Volume of Empty Space. *Journal of Cognitive Neuroscience*, *25*(7), 1078–1099.

Haggard, P., & Jundi, S. (2009). Rubber hand illusions and size-weight illusions: self-representation modulates representation of external objects. *Perception*, *38*(12), 1796–

1803.

Harris, C. S. (1965). Perceptual adaptation to inverted, reversed, and displaced vision. *Psychological Review*, *72*(6), 419–444.

Heim, C., & Nemeroff, C. B. (2001). The role of childhood trauma in the neurobiology of mood and anxiety disorders: preclinical and clinical studies. *Biological Psychiatry*, *49*(12), 1023–1039.

Held, R. (1961). Exposure-history as a factor in maintaining stability of perception and coordination. *The Journal of Nervous and Mental Disease*, *132*, 26–32.

Held, R., & Hein, A. V. (1958). Adaptation of disarranged hand-eye coordination contingent upon re-afferent stimulation. *Perceptual and Motor Skills*, *8*(3), 87.

Hochberg, C. B., & Hochberg, J. E. (1952). Familiar Size and the Perception of Depth. *The Journal of Psychology*, *34*(1), 107–114.

Hochberg, J. E., & McAlister, E. (1955). Relative Size vs. Familiar Size in the Perception of Represented Depth. *The American Journal of Psychology*, *68*(2), 294.

Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation(s) of peripersonal space. *Cognitive Processing*, *5*(2), 94–105.

Howard, I. P., Craske, B., & Templeton, W. B. (1965). Visuomotor adaptation to discordant exafferent stimulation. *Journal of Experimental Psychology*, *70*, 189–91.

Howe, M. L., & Courage, M. L. (1993). On resolving the enigma of infantile amnesia. *Psychological Bulletin*, *113*(2), 305–326.

Hurley, S., & Noë, A. (2003). Neural Plasticity and Consciousness. *Biology and Philosophy*, *18*(1), 131–168.

Itoh, K., Fujii, Y., Kwee, I. L., & Nakada, T. (2005). MT+ W V5 Activation without Conscious Motion Perception: A High-Field fMRI Study. *Magnetic Resonance in Medical Sciences*, *4*(2), 69–74.

Jeannerod, M. (2006). *Motor cognition : what actions tell the self*. Oxford University Press.

Jiang, Y., Costello, P., & He, S. (2007). Processing of Invisible Stimuli: Advantage of Upright Faces and Recognizable Words in Overcoming Interocular Suppression. *Psychological Science*, *18*(4), 349–355.

Julian, J. B., Ryan, J., & Epstein, R. A. (2016). Coding of Object Size and Object Category in Human Visual Cortex. *Cerebral Cortex*, 1, bhw150.

Kalckert, A., & Ehrsson, H. H. (2012). Moving a rubber hand that feels like your own: dissociation of ownership and agency. *Frontiers in Human Neuroscience, 6*, 40.

Kalckert, A., & Ehrsson, H. H. (2014). The spatial distance rule in the moving and classical rubber hand illusions. *CONSCIOUSNESS AND COGNITION*, *30*, 118–132.

Kaunitz, L., Fracasso, A., & Melcher, D. (2011). Unseen complex motion is modulated by attention and generates a visible aftereffect. *Journal of Vision*, *11*(13), 10.

Kilteni, K., Maselli, A., Kording, K. P., & Slater, M. (2015). Over my fake body: body

ownership illusions for studying the multisensory basis of own-body perception. *Frontiers in Human Neuroscience*, *9*, 141.

Koivisto, M., Mäntylä, T., & Silvanto, J. (2010). The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *NeuroImage*, *51*(2), 828–834.

Konen, C. S., & Kastner, S. (2008). Two hierarchically organized neural systems for object information in human visual cortex. *Nature Neuroscience*, *11*(2), 224–231.

Kovács, I., Papathomas, T. V, Yang, M., & Fehér, A. (1996). When the brain changes its mind: interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(26), 15508–15511.

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, *12*(4), 217–230.

Kravitz, J. H., & Wallach, H. (1966). Adaptation to displaced vision contingent upon vibrating stimulation. *Psychonomic Science*, *6*(10), 465–466.

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501. https://doi.org/10.1016/j.tics.2006.09.001

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*(11), 571–579.

Lee, M., Blake, R., Kim, S., & Kim, C.-Y. (2015). Melodic sound enhances visual awareness of congruent musical notes, but only if you can read music. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(27), 8493–8498.

Lee, S.-H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research*, *44*(10), 983–991.

Leibowitz, H., & Moore, D. (1966). Role of Changes in Accommodation and Convergence in the Perception of Size*. *Journal of the Optical Society of America*, *56*(8), 1120.

Levelt, W. J. M. (1965). *On Binocular Rivalry* (Doctoral dissertation, Van Gorcum, Assen).

Levy, J., & John. (1972). Autokinetic illusion: A systematic review of theories, measures, and independent variables. *Psychological Bulletin*, *78*(6), 457–474.

Linkenauger, S. A., Leyrer, M., Bülthoff, H. H., Mohler, B. J., Carroll, L., Linkenauger, S., … Masson, M. (2013). Welcome to Wonderland: The Influence of the Size and Shape of a Virtual Hand On the Perceived Size and Shape of Virtual Objects. *PLoS ONE*, *8*(7), e68594.

Lloyd, D. M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain and Cognition*, *64*(1), 104–109.

Lloyd, D. M., Shore, D. I., Spence, C., & Calvert, G. A. (2002). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience*, *6*(1), 17–18.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, *380*(6575), 621–624.

Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science (New York, N.Y.)*, *245*(4919), 761–763.

Lunghi, C., & Alais, D. (2013). Touch interacts with vision during binocular rivalry with a tight orientation tuning. *PloS One*, *8*(3), e58754.

Lunghi, C., & Alais, D. (2015). Congruent tactile stimulation reduces the strength of visual suppression during binocular rivalry. *Scientific Reports*, *5*, 9413.

Lunghi, C., Binda, P., & Morrone, M. C. (2010). Touch disambiguates rivalrous perception at early stages of visual analysis. *Current Biology, 20*(4), R143-4.

Lunghi, C., & Morrone, M. C. (2013). Early interaction between vision and touch during binocular rivalry. *Multisensory Research*, *26*(3), 291–306.

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: a human navigation network. *Science (New York, N.Y.)*, *280*(5365), 921–924.

Maidenbaum, S., Abboud, S., & Amedi, A. (2014) Sensory substitution: closing the gap between basic research and widespread practical visual rehabilitation. *Neuroscience & Behavioral Reviews, 41*, 3-15.

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, *191*(1), 1–10.

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is That Near My Hand? Multisensory Representation of Peripersonal Space in Human Intraparietal Sulcus. *Journal of Neuroscience*, *27*(4), 731–740.

Marino, B. F. M., Stucchi, N., Nava, E., Haggard, P., & Maravita, A. (2010). Distorting the visual size of the hand affects hand pre-shaping during grasping. *Experimental Brain Research*, *202*(2), 499–505.

Mark, L. S. (1987). Eyeheight-scaled information about affordances: a study of sitting and stair climbing. *Journal of Experimental Psychology. Human Perception and Performance*, *13*(3), 361–70.

Maruya, K., Watanabe, H., & Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *Journal of Vision*, *8*(11), 7.1-11.

Maruya, K., Yang, E., & Blake, R. (2007). Voluntary action influences visual competition. *Psychological Science*, *18*(12), 1090–1098.

Mastria, G., Mancini, V., Viganò, A., & Di Piero, V. (2016). Alice in Wonderland Syndrome: A Clinical and Pathophysiological Review. *BioMed Research International*, 8243145.

Mather, G., & Smith, D. R. R. (2002). Blur Discrimination and its Relation to Blur-Mediated Depth Perception. *Perception*, *31*(10), 1211–1219.

Mckee, S. P., & Smallman, H. S. (1998). Size and speed constancy. In V. Walsh & J. Kulikowski (Eds.), *Perceptual Contancy* (pp. 373–408). Cambridge: Cambridge University Press.

Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*, *4*(7), 539–51.

Morrison, C. M., & Conway, M. A. (2010). First words and first memories. *Cognition*, *116*(1), 23–32.

Moser, E. I., Kropff, E., & Moser, M.-B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, *31*(1), 69–89.

Mueller, T. J., & Blake, R. (1989). A fresh look at the temporal dynamics of binocular rivalry. *Biological Cybernetics*, *61*(3), 223–232.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, *9*(3), 429–434.

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. *NeuroImage*, *42*(4), 1669–1677.

Nava, E., Steiger, T., Röder, B., Spence, C., & Röder, B. (2014). Both developmental and adult vision shape body representations. *Scientific Reports*, *4*, 6622.

Noë, A. (2004). *Action in Perception*. Cambridge: MIT Press.

Noë, A. (2010). Vision without representation. In N. Gangopadhyay, M. Madary, & F. Spicer (Eds.), *Perception, Action, and Consciousness*.

Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(20), 11120–11124.

O'leary, A., & Wallach, H. (1980). Familiar size and linear perspective as distance cues in stereoscopic depth constancy. *Perception & Psychophysics*, *27*(2), 131–135.

O'Shea, R. P., Blake, R., & Wolfe, J. M. (1994). Binocular Rivalry and Fusion under Scotopic Luminances. *Perception*, *23*(7), 771–784.

Ooi, T. L., & He, Z. J. (1999). Binocular rivalry and visual awareness: the role of attention. *Perception*, *28*(5), 551–574.

Paffen, C. L. E., & Alais, D. (2011). Attentional Modulation of Binocular Rivalry. *Frontiers in Human Neuroscience*, *5*, 105.

Paffen, C. L. E., Alais, D., & Verstraten, F. A. J. (2006). Attention speeds binocular rivalry. *Psychological Science*, *17*(9), 752–756.

Petkova, V. I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., & Ehrsson, H. H. (2011). From Part- to Whole-Body Ownership in the Multisensory Brain. *Current Biology*, *21*(13), 1118–1122.

Petkova, V. I., & Ehrsson, H. H. (2008). If I Were You: Perceptual Illusion of Body Swapping. *PLoS ONE*, *3*(12), e3832.

Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The Perspective Matters! Multisensory Integration in Ego-Centric Reference Frames Determines Full-Body Ownership. *Frontiers in Psychology*, *2*, 35.

Petkova, V. I., Zetterberg, H., Ehrsson, H. H., Farne, A., & Roland, P. (2012). Rubber

Hands Feel Touch, but Not in Blind Individuals. *PLoS ONE*, *7*(4), e35912.

Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, *3*(11), 1153–1159.

Proffitt, D. R. (2006). Embodied Perception and the Economy of Action. *Perspectives on Psychological Science*, *1*(2), 110–122.

Proffitt, D. R., Bhalla, M., Gossweiler, R., & Midgett, J. (1995). Perceiving geographical slant. *Psychonomic Bulletin & Review*, *2*(4), 409–428.

Proffitt, D. R., Stefanucci, J., Banton, T., & Epstein, W. (2003). The role of effort in perceiving distance. *Psychological Science*, *14*(2), 106–112.

Rizzolatti, G., & Sinigaglia, C. (2008). *Mirrors in the brain : how our minds share actions and emotions*. Oxford University Press.

Rogers, B., & Graham, M. (1979). Motion Parallax as an Independent Cue for Depth Perception. *Perception*, *8*(2), 125–134.

Rohde, M., Di Luca, M., Ernst, M. O., Gibson, S., & Bradshaw, J. (2011). The Rubber Hand Illusion: Feeling of Ownership and Proprioceptive Drift Do Not Go Hand in Hand. *PLoS ONE*, *6*(6), e21659.

Rubin, D. C. (1982). On the retention function for autobiographical memory. *Journal of Verbal Learning and Verbal Behavior*, *21*(1), 21–38.

Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, *13*(7), 2–2.

Sampaio, E., Maris, S., & Bach-y-Rita, P. (2001). Brain plasticity: "Visual" acuity of blind persons via the tongue. *Brain Research*, *908*(2), 204–207.

Shimada, S., Fukuda, K., & Hiraki, K. (2009). Rubber Hand Illusion under Delayed Visual Feedback. *PLoS ONE*, *4*(7), e6185.

Shulman, G. L., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Petersen, S. E., & Corbetta, M. (1999). Areas involved in encoding and applying directional expectations to moving objects. *The Journal of Neuroscience*, *19*(21), 9480–96.

Singer, G., & Day, R. H. (1966). Spatial adaptation and aftereffect with optically transformed vision: effects of active and passive responding and the relationship between test and exposure responses. *Journal of Experimental Psychology*, *71*(5), 725–831.

Sobel, K. V, & Blake, R. (2002). How context influences predominance during binocular rivalry. *Perception*, *31*(7), 813–824.

Stefanucci, J. K., & Geuss, M. N. (2009). Big people, little world: the body influences size perception. *Perception*, *38*(12), 1782–1795.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, *9*(4), 255–266.

Stein, T., Sterzer, P., & Peelen, M. V. (2012). Privileged detection of conspecifics: Evidence

from inversion effects during continuous flash suppression. *Cognition*, *125*(1), 64–79.

Stratton, G. M. (1897). Vision without inversion of the retinal image. *Psychological Review*, *4*(4), 341.

Swanston, M. T., & Gogel, W. C. (1986). Perceived size and motion in depth from optical expansion. *Perception & Psychophysics*, *39*(5), 309–326.

Taylor, J. G. (1962). *The behavioral basis of perception.* New Haven: Yale University Press.

Taylor, J. G. (1965). The behavioral basis of perceived size and distance. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, *19*(1), 1–14.

Taylor, J. G. (1968). Perception as a Function of Behaviour. *Studies in Logic and the Foundations of Mathematics*, *52*, 431–436.

Todd, J. (1955). The syndrome of Alice in Wonderland. *Canadian Medical Association Journal*, *73*(9), 701–704.

Tong, F., & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, *411*(6834), 195–199.

Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, *10*(11), 502–511.

Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, *204*(3), 343–352.

Tsakiris, M., & Haggard, P. (2005). The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(1), 80–91.

Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, *15*(2), 423–32.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101.

Tsuchiya, N., Koch, C., Gilroy, L. A., & Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *Journal of Vision*, *6*(10), 1068–1078.

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80*(5), 352.

van der Hoort, B., Guterstam, A., & Ehrsson, H. H. (2011). Being barbie: The size of one's own body determines the perceived size of the world. *PLoS ONE*, *6*(5), e20195.

van Ee, R., van Boxtel, J. J. A., Parker, A. L., & Alais, D. (2009). Multisensory congruency as a mechanism for attentional control over perceptual selection. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(37), 11641–11649.

van Ee, R., van Dam, L. C. J., & Brouwer, G. J. (2005). Voluntary control and the dynamics

of perceptual bi-stability. *Vision Research*, *45*(1), 41–55.

van Loon, A. M., Scholte, H. S., van Gaal, S., van der Hoort, B. J. J., & Lamme, V. A. F. (2012). Agonist Reduces Visual Awareness: A Masking–EEG Experiment. *Journal of Cognitive Neuroscience, 24*(4), 965-974.

Vidal, M., & Barrès, V. (2014). Hearing (rivaling) lips and seeing voices: how audiovisual interactions modulate perceptual stabilization in binocular rivalry. *Frontiers in Human Neuroscience*, *8*(677).

von Helmholtz, H. L. F. (1925). *Treatise on Physiological Optics*. New York: Dover Press.

von Holtz, E., & Mittelstaed, H. (1950). The Principle of Reafference: Interactions Between the Central Nervous System and the Peripheral Organs. *Naturwissenschaften*, (27), 464–476.

Wade, N. J., De Weert, C. M. M., & Swanston, M. T. (1984). Binocular rivalry with moving patterns. *Perception & Psychophysics*, *35*(2), 111–122.

Wallach, H., & O 'Connell, D. N. (1953). The kinetic depth effect. *Journal of Experimental Psychology*, *45*(4), 205–217.

Ward, J., & Meijer, P. (2010). Visual experiences in the blind induced by an auditory sensory substitution device. *Consciousness and Cognition*, *19*(1), 492–500.

Warren, W. H. (1984). Perceiving affordances: visual guidance of stair climbing. *Journal of Experimental Psychology. Human Perception and Performance*, *10*(5), 683–703.

Warren, W. H., & Whang, S. (1987). Visual guidance of walking through apertures: body-scaled information for affordances. *Journal of Experimental Psychology. Human Perception and Performance*, *13*(3), 371–383.

Welch, R. (1978). *Perceptual modification: Adapting to altered sensory environments*. New-York: Academic Press.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(20), 11125–11129.

Witt, J. K., Linkenauger, S. A., Bakdash, J. Z., & Proffitt, D. R. (2008). Putting to a bigger hole: golf performance relates to perceived size. *Psychonomic Bulletin & Review*, *15*(3), 581–585.

Witt, J. K., & Proffitt, D. R. (2005). See the ball, hit the ball: Apparent ball size is correlated with batting average. *Psychological Science, 16*(12), 937-938.

Witt, J. K., Proffitt, D. R., & Epstein, W. (2005). Tool Use Affects Perceived Distance, But Only When You Intend to Use It. *Journal of Experimental Psychology: Human Perception and Performance, 31*(5), 880-888.

Wolf, M., & Hochstein, S. (2011). High-Level Binocular Rivalry Effects. *Frontiers in Human Neuroscience*, *5*(129).

Yang, E., & Blake, R. (2012). Deconstructing continuous flash suppression. *Journal of Vision*, *12*(3), 8–8.

Yang, E., Brascamp, J., Kang, M. S., & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in Psychology*, *5*, 724.

Yu, K., & Blake, R. (1992). Do recognizable figures enjoy an advantage in binocular rivalry? *Journal of Experimental Psychology: Human Perception and Performance*, *18*(4), 1158–1173.

Zhou, G., Zhang, L., Liu, J., Yang, J., & Qu, Z. (2010). Specificity of face processing without awareness. *Consciousness and Cognition*, *19*(1), 408–412.

Zhou, W., Jiang, Y., He, S., & Chen, D. (2010). Olfaction Modulates Visual Perception in Binocular Rivalry. *Current Biology*, *20*(15), 1356-1358.